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SCIENTIFIC WEATHER FORECASTING.

THERE is hardly any kind of writing which so abounds with pitfalls as the history of scientific progress. Questions of priority arise in every few lines, and a writer who is worth his salt knows two things—(i.) that he had better not write at all unless he can improve greatly upon what has been written before, and (ii.) that the next man who attempts it ought to do better still.

Weather forecasting, after a fashion, has gone on for thousands of years, and some of the rules of the Hebrews, Greeks and Romans, preserved in the Bible and in the writings of Aristotle, Theophrastus and Aratus, may justly be called scientific, as they represent definite conclusions drawn from physical facts. The special object of the present article is historical, to show how Scientific Weather Forecasting became possible, rather than how it is at present being done in nearly every country in the world.

But, by those who have not previously considered the subject, the historical points will be more readily appreciated if a very brief and elementary sketch be given of the method now adopted.

Each country has a central office and a considerable number of small observatories—stations they are generally called—scattered widely apart over its territories, preferably on the sea-coast, but always at places whence there is electro-telegraphic communication with the central office. At each of these stations there is at least one good baro-

meter and thermometer—at the majority of them there are a full set of meteorological instruments and some in duplicate. The observer has to read the instruments at specified hours, and to telegraph the results to the central office.

At the central office, the observations from each station are (after the application of any necessary corrections) marked upon a map; the barometer and thermometer in figures, the wind by an arrow flying with the wind, and with barbs proportional to the strength of the wind. These entries are made over the spot upon the map which represents the station whence those data came. When all the reports have arrived, lines are drawn joining places at which the barometric pressure is the same (isobars), and through those of which the temperature is the same (isotherms). A distinct relation is immediately evident between these isobars and the arrows representing the direction and force of the wind. Roughly, the arrows are parallel with the isobars, and they are more barbed—*i.e.*, the wind is stronger—the closer the isobars are together.

Generally these isobars are curved, and enclose an area either of low or of high barometric pressure. In the former case there is said to be a cyclone; in the latter, an anti-cyclone. If the central barometric pressure be very low and the isobars close together, a violent storm is in progress; if the central pressure be high and the isobars wide apart there is a calm, and, in winter, generally a fog.

These cyclonic and anti-cyclonic systems move about, chiefly in easterly directions, but they do not move with the speed of the telegraph, and, consequently, if it were possible to know the direction, and the rate, of their movement, it would be possible to state where the centre would be at a given time, and from that knowledge to state what weather would prevail at any given spot, because the weather characteristics of each quadrant of a cyclone are known. The difficulty for the forecaster is, to tell in what direction and at what speed the system will move, and whether it will increase or decrease in intensity. This is not easy even in the United States, where, generally, the systems can be watched from their birth in the Rocky Mountains until they pass away on to the Atlantic; but for the British Isles and

for France, which have no stations to the West of them, it is extremely difficult. There are, moreover, "V shaped depressions," "secondaries," and other varieties of distribution of pressure to be detected and taken into account, so that on the whole a British forecaster probably requires boldness as much as he needs knowledge.

From the above very brief sketch of the principles of Scientific Weather Forecasting, it will be seen that the essentials are—(i.) Knowledge of the general principles of atmospheric circulation; (ii.) the use of weather maps; (iii.) the use of the electric telegraph.

The fact that storm systems travel towards the east was noticed at a very early date. Mr. R. H. Scott, F.R.S. (1) says:—

"The earliest notice of it which we can discover is an entry on the map of Virginia, published in 1747 by Lewis Evans, to the effect that 'all our great storms begin to leeward'. Franklin, in 1760, followed in the same strain, but it appears that his attention had been caught at an earlier period, in 1743, by the fact of his being prevented at Philadelphia, by the clouds brought by a hurricane, from observing a lunar eclipse, while the eclipse was seen at Boston, which lies farther to the north-eastward, before the storm came on."

The first proposals towards the existing arrangements seem to have been those of Lavoisier (2) about 1780, but his suggestion included little knowledge of the laws of atmospheric circulation, no weather map, and no electric telegraph. He knew that a falling barometer generally indicated wet weather, and a rising one fine weather, and suggested that predictions based upon the motion of a single barometer might be sent daily for publication in a newspaper. Romme in 1793 (3) carried the proposal farther, and suggested the use of Chappe's Aerial Telegraph to "enable physicists to foresee the arrival of storms, and to give notice of them to the ports and to farmers".

It is incapable of proof, but not improbable, that the foregoing suggestions, and the investigation next to be mentioned, were indirectly connected with the great work carried out about that date by the Meteorological Society

of the Palatinate in the publication of the Mannheim Ephemerides. In 1801 appeared Colonel Capper's work (4) upon the results of his observations upon the coast of Coromandel, in which he lays down the circular character of the motion of the winds.

In 1820 Professor H. W. Brandes of Breslau published an important work (5) in which he discussed, with great labour and skill, daily records for the year 1783 from thirty stations, twenty-eight in Europe and two in America. It is curious to notice how closely he approached modern methods; for instance, a storm and barometric depression passed from the British Isles to Berlin from about the 6th to the 9th of February, and although in his book he does not give a chart, it is almost certain that he must have drawn one, with something identical in appearance with our modern isobars. The modern practice of reducing barometer readings to their equivalent sea level pressures had not been thought of, but instead, Professor Brandes adopted the plan (much later employed by Buijs Ballot) of expressing the readings as departures from the average. To show how thoroughly he had seized the idea of isobars a few words must be quoted:—

"Am tiefsten, nämlich 14 Linien unter der Mittelhöhe stand das Barometer in Lyndon in Rutlandshire. Die gegend, wo es 13½ Linien unter der Mittelhöhe stand, lässt sich durch eine Linie bezeichnen, die etwas westlich von Franeker, genau über Amsterdam und dann vermuthlich das südliche England geht. Die Linie wo es 13 Linien zu tief stand, geht noch oberhalb Mittelburg, über den Canal, nach dem französischen Hafen St. Malo."

Professor Brandes similarly traces the lines joining the gradually less and less depressions until he reaches a depression of only three lines at Bologna and Rome. In another place he regrets that he had not sufficient information similarly to study the direction and strength of the wind, he says that where the barometer was lowest the wind was strongest, that the depression occurred earlier on the Atlantic coast than in the East, and he anticipated the modern idea of barometric gradient by comparing the depression at different places and dividing it by their dis-

tance and then trying to get out the resultant velocity of the wind.

All this be it remembered was published in 1820, and therefore was probably done some years before. In 1830 Redfield in the United States announced that (i.) storms were approximately circular (ii.) travelled north-eastwards (iii.) increased in strength towards the centre; but (iv.) became calm at the centre, and he illustrated this by a diagram (6).

From about 1830, Col. (afterwards Sir Wm.) Reid was at Bermuda, and in his *Law of Storms* (7) he says:—

"A very interesting mode of testing the Law of Storms is that of considering the probable line of progression of gales in their passage. It was thus that I (Col. Reid) was in the habit of studying the winds at Bermuda for nearly eight years, and that Mr. Redfield has studied them at New York for a much longer period. In September, 1839, Mr. Redfield wrote to me from New York, when he first heard of the gale of that year, that he thought it must have passed over Bermuda; and this was before he could have heard from these islands. A reference to the plate will show how correct his judgment was, for the centre touched the westermost part of the islands."

From 1830 onwards, the construction of weather maps was general with leading meteorologists, such as Espy, Piddington, Redfield and Reid; but these, it must be remembered, all referred to dates far anterior to their construction. The electric telegraph was not invented until 1837, and it was not until a much later date that its use was sufficiently extensive and cheap to allow meteorologists to avail themselves of it.

The first proposal for the use of the telegraph, and of synchronous observations for weather forecasting, which we can trace, was by Carl Kreil in 1842, when he was assistant at Prague Observatory (8). It is much too long for reproduction, but points out the necessity for having distant stations; that the optical telegraph was scarcely sufficiently rapid and could not be used at night, but that the recently discovered electro-magnetic telegraph, as soon as it had been brought into general use, would precisely meet the case, and he illustrates the method by the passage of the

storm of 17th and 18th July, 1841, from South Italy to Prague in about thirty hours.

Closely connected with weather forecasting are arrangements on the coast for indicating to passing vessels the height of the barometer, or the character of weather likely to prevail. The earliest note of this kind which we have seen was in a fragment of the *Carnarvon Herald* (9) for 1841 or 1842, in which an anonymous writer proposed the erection of an indicator with a circular dial, 3 ft. in diameter, divided somewhat like a wheel barometer, and with a bar (corresponding in position to the hand of a wheel barometer, but) projecting 1 ft. 6 in. beyond the dial.

This was a proposal only; five years later Col. Reid had another arrangement in actual work. We give his account verbatim (10):—

"In 1847 I had the satisfaction of establishing signals at Barbados to give warning of approaching hurricanes, and of publishing at the same time suggestions as to the direction in which ships should be steered when quitting Carlisle Bay at the setting in of a hurricane".

Then follows a reprint of the official notice, whence we can quote only the first four paragraphs:—

"A barometer is kept and registered at the principal police station at Bridgetown, Barbados, and notice will be given to the captain of the port when it falls. On the captain of the port rests the responsibility of causing signals to be hoisted that the barometer indicates bad weather.

"One ball at the masthead of the signal-posts is to signify that the barometer is falling, and should be carefully watched.

"If the barometer continues to fall and the weather appears threatening, a second ball will be hoisted at the masthead.

"As the indications of the weather become alarming, these two balls will be gradually lowered until they are only half-mast high."

Until within the last thirty or forty years, meteorologists in one country knew far too little of what was being done in other countries. For instance, it is almost certain that neither Fitz Roy, Glaisher, nor Le Verrier ever read the statement by Kreil, which we have mentioned earlier in this

article, and which had been printed years before they took action in the matter. This lack of inter-communication, and difficulties arising from the use of different languages, should not be forgotten, because it makes many discoveries really independent which, looked at chronologically, appear successive.

The first actual use of the electric telegraph for the transmission of information respecting the weather seems to have been in America, as Professor Henry, the Secretary of the Smithsonian Institution, in 1849, personally requested the telegraph companies to direct their operators to replace in their regular morning despatches the signal "OK" (by which they were accustomed to announce that their lines were in order) by such words as "fair," "cloudy," etc., thus giving without additional trouble, and as concisely as possible, a summary of the condition of the weather at the different stations, and which should be communicated to him (11).

This, it will be noticed, was weather *only*, and no map was made representing the information. Wind direction was, we believe, not sent to Washington till 1858, and at that date the information was marked on a large map by moveable discs.

Synchronously with Professor Henry's action in the United States, or possibly slightly before it, Mr. Glaisher, F.R.S., was organising, by the joint action of the Electric Telegraph Company, the Railway Clearing House, and the proprietors of the *Daily News*, a really scientific system in this country. Furnished with a pass over nearly every railway in the country, he went to all the terminal stations of the Electric Telegraph Company, and to many of the intermediate ones, determined a meridian line for each and instructed the clerks as to observing the direction of the wind, and reporting the state of the weather.

The first publication was in the *Daily News* of 14th June, 1849, when a table was inserted giving the direction and strength of the wind and the state of the weather at thirteen stations, and the following footnote. "As explained elsewhere[1] the very extensive arrangements for making this table complete have not yet been concluded. In a short time we shall

[1] But no such explanation can be found.

present daily returns from thirty-nine stations extending from Plymouth to Glasgow and from Yarmouth to Holyhead."

In 1851 came the Great Exhibition, and the exhibit of the Electric Telegraph Company consisted of a large map on which were daily indicated the direction of the wind and the state of the weather at about thirty of their stations, and also of daily reproductions by lithography which were sold at a penny a copy. These were the first maps of current weather ever issued, and notwithstanding that there are no isobars and the barometer readings were not reduced to sea level (although Mr. Glaisher had, in the tables supplied to the Registrar General, adopted this excellent plan as early as 1849), the clean sharpness of the printing makes these maps extremely interesting. Unfortunately their publication ceased when, or slightly before, the Exhibition closed. The issue extended from 8th August to 11th October, 1851, with the exception of Sundays. A few perfect copies of the entire set have been preserved.

Placing ourselves in imagination in the latter part of 1851, we find nearly every part of the modern system suggested, or in operation; the circular theory of storms, their easterly progression, their calm centre, isobars and the dependence of wind force on their proximity (now called the barometric gradient), the construction of weather maps from synchronous observations on the same day, the prediction of future based upon the knowledge of existing weather, and the communication to ships of information gained upon land.

Consequently though we should be the last to depreciate the work of Buijs Ballot, Le Verrier, Fitz Roy and their successors, and though doubtless much of their work was original with them, still there is no need now to dwell much upon it.

We believe that the first Government to take action in the matter of collecting data by telegraph was that of Holland, on the recommendation of Buijs Ballot, in or about 1855, and that they very shortly followed this by sending announcements of coming storms.

France, at the suggestion of Le Verrier, organised an analogous system in the same year.

England came third, beginning under Admiral Fitz

Roy, as the result of a suggestion by Le Verrier in 1860. It will probably be of interest to reproduce from the *Times* the first daily weather report issued by the Meteorological Office, that for 5th September, 1860.

THE WEATHER.

METEOROLOGICAL REPORTS.

Sept. 5, 9 A.M.	B.	E.	M.	D.	F.	C.	✢
Greenock	30·21	59	58	W.S.W.	2	0	b.
Berwick		59	58	W.	2	—	—
Galway	30·34	59	58	N.W.	2	8	b.c.
Hull	30·15	59	57	W.	2	2	b.
Yarmouth	30·15	58	57	N.W.	3	0	b.
London	30·26	60	55	W.	3	3	b.c.
Dunkirk	30·32	58	52	W.	0	0	b.
Portsmouth	30·30	54	54	N.	1	4	b.c.
Plymouth	30·20	60	59	W.	1	3	b.c.
Penzance		64	62	N.	2	2	b.o.
Cherbourg	30·32	60	53	—	—	2	b.c.
Havre		54	—	W.	0	1	b.m.
Jersey	30·30	61	57	N.	2	5	b.c.
Brest	30·09	59	50	N.W.	—	3	b.c.

Explanation.

B. Barometer, corrected and reduced to freezing, at mean sea level. E. Exposed thermometer. M. Moistened bulb. D. Direction (true) of wind. F. Force (0 to 12). C. Cloud (0 to 10). ✢ Initial letter of appearance in sky (by Beaufort method).

M. O.

(By Electric and International Telegraph.)

Wind and Weather Report at 8 o'clock Yesterday Evening.

Inverness, S.W.; fine.
Aberdeen, N.; dull.
Dundee, calm; fine.
Edinburgh, W.; foggy.
Berwick, N.; foggy.
Newcastle-on-Tyne, W.; fine.
Hartlepool, S.E.; fine.
York, N.; fine.
Hull, E.; fine.
Derby, N.; dull.
Peterborough, N.E.; dull.
Yarmouth, N.N.E.; dull.
Harwich, N.; fine.
Manchester, N.W.; dull.
Southampton, calm; cloudy.
Weymouth, calm; cloudy.
Plymouth, N.W.; fine.
Bristol, E.; fine.
Cardiff, W.N.W.; fine.
Holyhead, N.W., calm; cloudy.
Liverpool, W.N.W.; cloudy.
Glasgow, N.; fine.
Jersey, N.W.; very fine.
Colchester, W.; fine.
Leeds, W.; fine.

It will be noticed that there are in the above two reports—Admiral Fitz Roy's for 9 A.M., 5th September, 1860, and the Telegraph Company's report for 8 P.M. on the same day.

Within six months of the receipt of his first telegrams Admiral Fitz Roy had gained sufficient confidence in his organisation to issue a warning of a coming storm (February, 1861), and within a year he began to issue (August, 1861) forecasts of coming weather. This rapid progress drew public attention to the subject and, but for the want of funds, this country would (as it so often has done) have gone ahead of its own Government, and again by private enterprise been first of any country in the world to produce a daily telegraphic weather map. We should, if possible, have given the names of those who promoted the company which desired to do this, but we have only the prospectus and the map for 5th August, 1861, and it bears no name. The scheme was extremely ingenious, and the map could have been issued in London within three hours of the observations being taken in any part of the British Isles. The map was about twenty inches by fifteen inches, and contained records from sixty-two stations well distributed from Penzance to Nairn, and from Galway to Yarmouth. The map was to be printed from an ordinary press, the outline names of stations, etc., being on a large block, with an octagonal hole for each station, through which hole the appropriate symbol was passed, and when all had been put in position, the map was ready for printing. The symbols were very simple, three varieties of outline showed whether the barometer was rising, stationary or falling, the letter C and four varieties of arrows showed the force of the wind, while its direction was shown by that of the arrows, and five systems of ground (dots, rings, etc.), showed whether the sky was clear, partly cloudy, overcast, showery, or continuously rainy. Some one must have lost heavily, for all the necessary instruments were made by Negretti and Zambra, verified by Mr. Glaisher, and conveyed to their destinations, the map and symbols were prepared and engraved, but the funds for the issue of the *Daily Weather Map and Journal* were not obtained, Admiral Fitz Roy would not (or was not allowed to) help, and so the scheme fell through, and England which had been the first to produce one was left without a daily weather map for

twenty-one years, until at last in 1872 the English Meteorological Office consented to issue one.

But in France Le Verrier was aware of the importance of such an issue from the first, and France published its first Daily Map of the Weather as early as 16th September, 1863, and the United States followed in January 1871, so that as regards official publication England was third instead of being first.

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G. J. SYMONS.

THE NATURAL HISTORY OF IGNEOUS ROCKS: I. THEIR GEOGRAPHICAL AND CHRONOLOGICAL DISTRIBUTION.

INTENDING in this and succeeding papers to glance at some of the modern aspects of petrology in relation to igneous rocks, we shall begin by considering briefly the distribution of the rocks in time and space. In studying the geology of particular regions this subject has often been passed over, even by eminent authorities, with but slight notice. Indeed it must be admitted that in general igneous rocks are accorded a rather unceremonious treatment. Too often they are relegated to an appendix in a memoir or monograph, as if they were without significance in the geological history of the district where they occur. They are indeed indicated as regards their situation on geological maps, but only with a colour denoting more or less correctly their petrographical nature. Often we see, on otherwise carefully drawn up maps, a common legend of "volcanic rocks," applied alike to Tertiary basalts and Palæozoic rhyolites and andesites. It is curious to note that while stratigraphy has, so far as the sedimentary rocks are concerned, replaced the old-fashioned "geognostic" maps by those expressing in the first place chronological sequence, no such change has been made in the mode of representing the igneous rocks. It is not a little instructive, as will be found by any one who will test it, to construct maps on which the igneous rocks, whether interbedded or intruded, are marked in the colours adopted for the stratified formations of like age. The distinction between intruded and interbedded, and, if desired, between acid and basic rocks, etc., can be rendered by different tints and hachures.

The subject is one of considerable importance to the physical geographer as well as to the geologist, if indeed these are to be regarded as two distinct individuals. Although volcanoes have been studied from a very early time, and in some respects with great thoroughness, some of the

most fundamental points concerning them are still involved in doubt. Their geographical and local distribution is one such question. It is a familiar fact that the arrangement of volcanic vents at the present day is in general a linear one, giving place in some regions to a disposition in groups; further, that the lines often correspond very evidently with coast-lines, while the groups are often island-groups. On these and other data some have based theories of the situation of the vents on lines of fracture in the earth's crust, while others have speculated upon an accession of sea-water as the proximate cause of volcanic eruptions; but such hypotheses rest at present upon a very slender basis of ascertained fact. Other questions arise when we examine the products ejected by modern volcanoes. On the one hand, we find throughout a vast tract, such as the Andes, all the volcanic rocks closely related in characters and departing but little from a central type; on the other hand, a small group, such as that of the Æolian Isles, may afford varieties of lava of widely diverse and highly special characters. To such problems a study of modern volcanoes alone can scarcely hope to bring a satisfactory solution. It is necessary to inquire whether some empirical laws which seem to hold good are not rather to be regarded as parts of larger principles, and to seek for an explanation of present anomalies by viewing them as survivals of a pre-existing state of things.

In such a course, as in not a few modern geological inquiries, we are reversing the maxim of the school of Hutton and Lyell. Instead of applying a knowledge of the processes now going on around us to elucidate the record of past ages, we are making use of the history of the past to explain the phenomena of the present. Geology is thus repaying some of the debt which she owes to Physical Geography.

The frequent close connection of plutonic and intrusive rocks with surface vulcanicity is now scarcely called in question, though, in the nature of the case, instances must be few in which such connection can be directly demonstrated. Special stress was laid on this point by Judd in

his study of the Tertiary igneous rocks of the Inner Hebrides, and similar conclusions have been arrived at by Lotti in Elba and by various other geologists in the Andes and elsewhere. Of special importance in this connection are the researches of Hague and Iddings on the rocks of the Comstock Lode in Nevada. The extensive mining operations at that place enabled them to make a comparative study of the rocks through a very considerable vertical range, and they conclusively established the gradual transition in characters from andesitic rocks consolidated under practically superficial conditions to the plutonic equivalents of those rocks formed at greater depths and in the heart of the mass. Of interest, too, is the close correspondence, shown by Iddings (1) in the Yellowstone Park district, between the intrusive porphyrites and diorites of Electric Peak and the breccias and lavas of Sepulchre Mountain. Speaking generally, the geological evidence warrants us in affirming that igneous intrusions have occurred in districts of volcanic outbursts, and are so related in point of time to the latter as to indicate an essential connection between the two phenomena.

The growth of opinion concerning the petrology of igneous rocks has been, in recent years, mainly around two central ideas, *viz.*, the close relation subsisting between igneous activity and movements of the earth's crust, and the production under proper conditions of various rock-types from one original rock-magma. Neither of these ideas is strictly a new one. The former was insisted upon long ago by von Buch and others; but while those writers regarded volcanic outbursts as the causes of disturbances of the strata, modern geologists take rather the converse view. Again, the conception of differentiation in molten rock-magmas is at least as old as Durocher's famous theory; but only recently has the idea been developed with any attempt at completeness, and the practical application of it to a particular group of associated rocks had scarcely been ventured upon before Brögger's studies in the Christiania basin.

It is with the former of the two ideas just mentioned that we are here concerned. The work of Suess, Lossen,

Bertrand and many others has now given us a sufficient general idea of the nature, situations and epochs of the most important crust-movements during the times contemplated by the stratigraphical geologist, and it is possible to discuss to some extent the relation to these movements of the known groups of igneous rocks, both intrusive and extrusive. This has been done summarily for the European area by Bertrand in a memoir, published in 1888, which may be taken as a model for this kind of investigation (2). In a more restricted region, the geological history of which is sufficiently well known, the comparison may be developed in greater detail. For an application to our own country the data are furnished by Sir A. Geikie's account of volcanic action within the British area, contained in his Presidential Addresses to the Geological Society in 1891-92, and supplemented, as regards the Tertiary igneous rocks, by his memoir of 1888 (*Trans. Roy. Soc. Edin.*), and by the various papers of Judd.

Bertrand distinguishes in Europe four great systems of folding and disturbance of the stratified rocks; the earliest, the so-called Huronian, being here added to the Caledonian, Hercynian, and Alpine systems already recognised. The regions affected by these disturbances form broad zones, limited on the map by sweeping curves; and the several zones, while partially overlapping one another, successively advance further towards the equator. It seems probable that the first, and perhaps also the last, of these four systems must eventually be further divided, but Bertrand's statement of the broad facts affords meanwhile a basis for important generalisations. To the Huronian system belong crust-movements of pre-Palæozoic and early Palæozoic age, the first effects of which are seen in the north-western Highlands of Scotland and along the Norwegian coast, though the region ultimately involved had a considerably wider extent. The Caledonian (Upper Palæozoic) disturbances affected the greater part of what are now the British Isles as well as a belt extending north-eastward through Scandinavia. The main zone of Hercynian folding, marking the close of Palæzoic time, extends eastward

from the South of England and Brittany through Central Europe to Saxony and Silesia. To the latest (Tertiary) epoch of disturbance belongs the great Alpine system of mountain-chains, with its extensions into Asia and Northern Africa. The author makes it clear that each of these great systems of crust-movement has its own suite of volcanic, intrusive, and plutonic rocks, developed within the limits of the disturbed region, and in a general sense contemporaneous with the folding.

That this contemporaneity of igneous activity with disturbance of the solid earth-crust is to be understood in a general sense will be easily apparent. It is certain that movements of the kind considered proceed with extreme slowness, being prolonged, interrupted, and resumed during long periods of time; and many observations go to prove that they are not simultaneously felt throughout their extent, but are gradually propagated in wave-like fashion through the crust of the earth. There is no difficulty in believing that the disturbances initiated in Eocene and Miocene times have in some regions not yet wholly subsided. Again the geological records of superficial volcanic action prove it in many districts to have been of long duration, with intervals of quiescence interrupted by renewed activity, and finally gradual extinction; while there is good reason for supposing that the intrusion and complete consolidation of, say, a large body of granite implies a lapse of time not always to be included within the limits of one geological period. Regarding then the four, or more, distinct times of folding, not as decisive epochs, but rather as prolonged ages, having, however, a more or less defined era of maximum energy, and allowing a similar latitude as regards the associated manifestations of igneous activity, we may expect to find that in some cases the eruptions connected with one system of crust-movements overlap in time those belonging to another system, and that perhaps in districts not very widely separated. In such cases the true relations may appear only on a comprehensive view, embracing, for instance, the whole of the European area. Thus in the Midland Valley of Scotland igneous activity connected

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with the Caledonian crust-movements was continued through a large part of the Carboniferous period and even in some districts into the Permian, while the Carboniferous and Permian igneous rocks occurring in many districts from the Loire Valley eastward to Saxony are clearly related to the Hercynian folding. It may be noted that, having regard to the petrographical characters of the rocks in question, the Scottish lavas and tuffs are mainly of basaltic nature, while acid types generally prevail among the volcanic rocks of the same general age within the Hercynian zone; although perhaps much weight should not be allowed to such considerations. The granites of Cornwall and Devon, it may be remarked, are to be grouped not with British occurrences farther north, but with those of Brittany, as members of the Hercynian series.

A point of equal importance is the frequent overlapping in space of the several zones of disturbance, or the tendency of a district already affected by a earlier set of movements to become involved in the operations of a later set. With this we may correlate the fact, emphasised by Geikie, that particular districts in the British Isles have been the theatre of a recrudescence of volcanic activity at several distinct and sometimes widely separated epochs. Numerous examples illustrating these two related principles might be cited in Scotland and Wales, and equally striking instances appear in other countries. Thus it is known that parts of the Alpine chains coincide with older lines of folding of Hercynian and perhaps greater age, and Bertrand has pointed out in the Tirolese area a belt of Permian and Triassic eruptive rocks branching off from the main Hercynian zone to follow exactly a line laid down as that of the "pre-Permian Alps" of that district. He has even maintained with much plausibility a tendency for anticlinal and synclinal axes of the newer folding to be not only parallel to, but actually superposed upon, like axes of the older folding. This hypothesis has attracted considerable attention owing to its important practical consequences. For instance, the search for coal in our south-eastern countries will be very materially forwarded if the folds of

the Mesozoic strata can be taken as an accurate guide to those of the older rocks which they conceal.

The close connection between crust-movements and igneous eruptions is exemplified not only by the constant association of igneous rocks with disturbed strata, but equally by the absence of such rocks from undisturbed districts. As instances of this we might point to very extensive tracts in Russia, the Mississippi basin, and other countries; the significance of the fact being in some cases heightened by contrast with neighbouring districts, where the same strata, involved in a disturbed zone, are found to contain intercalated volcanic formations or to be traversed by dykes or other intrusions.

We are brought then to regard igneous rocks in general as in no wise meaningless interpolations in the stratigraphical sequence, but rather as closely bound up with the geological history of the districts in which they occur, and often in intimate relation with folds, faults, unconformities, and other geological accidents. Broadly viewed, they occur within large but defined regions of the globe co-extensive with the areas of operation of the crust-movements of which those same accidents are witnesses. Further, we are often able to divide one of these great regions into provinces of smaller, but still in some cases very extensive, dimensions; these provinces being also defined with reference to the folding of the region, while their individuality is often marked by peculiarities, petrographical or otherwise, in which they differ from one another. The eruptions in one such province are not necessarily contemporaneous in a strict sense with those in another, and we shall see that different stages of development may co-exist in neighbouring provinces of one region. In one province, at least in the later stages of its history, we may recognise districts presenting distinctive features of their own and including perhaps one or more volcanic centres.

To illustrate what we have styled provinces of eruptive rocks we may take those belonging to the Alpine system in Europe. Within the zone of Alpine folding itself are four well-defined provinces; the Tyrrhenian, extending from the

western portion of Italy westward, so as to include part of the African coast and the Cabo de Gata district in Spain; Hungary and Transylvania; Servia and Rhodope; and the Ægean, continuous towards the east with part of Asia Minor. Each of these areas is embraced by mountain-chains belonging to the Alpine system, and they occupy indeed the spaces left between the several branches where least compressed. Another group of provinces, in some cases less sharply defined, occurs just outside the northern border of the main belt of folding. To this belong Auvergne and Cantal; the Eifel and the Siebengebirge; Hesse, the Vogelsgebirge, and the Rhön; the Saxon Mittelgebirge, and Bohemia. Within the areas thus defined are districts containing volcanoes which have not long been extinct, while in the former group of provinces, *viz.*, in the lobes of the Mediterranean embraced by mountain-chains of the Alpine system, vulcanicity is still active at several centres.

It will be observed that the foregoing summary of the distribution of Tertiary and post-Tertiary igneous activity in this quarter of the globe is incomplete, in that it makes no mention of the British Islands. Antrim and the Inner Hebrides, with their Eocene igneous rocks, form part of a great province extending northwards into the Arctic regions, within which vulcanicity has been operative in Tertiary times, and in some districts has not yet died out. Further, this Brito-Icelandic province is itself only part of a region which also includes the Azores, Canaries, Cape Verd Islands, Ascension, St. Helena, and Tristan d'Acunha, with parts of the Portuguese and African coasts, thus stretching along the whole Atlantic border of the Old World. Unlike the others already noticed this region has a general meridional trend. Bertrand sees in this extra-Alpine region of Tertiary igneous rocks the illustration of a new principle, the operation of which is not to be seen, or at least is not clearly marked, in the earlier geological periods. The igneous rocks are still related to crust-movements, but in this case to those greater movements of which oceanic depressions and continental elevations are the results. We have indeed scattered relics

of a belt girdling the Atlantic, analogous to the much better defined "Circle of Fire" which surrounds the Pacific Ocean. Judd, following Nordenskjöld, long ago suggested that the volcanic rocks seen at so many points from Jan Mayen to Tristan d'Acunha may be regarded as portions of a ridge, now for the most part submerged, bordering the eastern continents as the volcanic belt of the Rocky Mountains, Cordilleras, and Andes does the western.

Taking now as an established principle the intimate relation between igneous rocks and crust-movements, whether of the mountain-building or of the continent-building order, we pass on to another branch of our subject, *viz.*, the idea of historical sequence in the various phenomena of igneous action. This may be viewed either from the physical or from the petrological aspect. The conception of a "life-history" of a volcano, divided into successive stages of development and decline, is not a new one, and it is capable of extension to districts, provinces, and regions of igneous rocks. The question whether such traces of a connected history are to be detected in the geological record as a whole is a more dubious one, and need not detain us at present. Those who see in this record evidences of a general decline in the energy of vulcanicity from Archæan times to the present day have perhaps been influenced to some extent by *a priori* reasoning on the physics of a gradually cooling globe.

The earlier stages in the igneous history of a disturbed region seem to have been marked usually by the intrusion of considerable bodies of molten magmas, often by violent superficial outbursts of a paroxysmal character, and generally by the approximately simultaneous extrusion of great quantities of lava at various centres over very extensive areas. The closing event as regards intrusive rocks has been the injection of fissures by dykes, which are often seen to traverse the earlier plutonic and large intrusive masses; while surface outbursts have been restricted in their later stages to diminishing and often isolated districts. The modern volcanoes of the Mediterranean area and of

Iceland, etc., regarded as survivals of the Tertiary volcanic era, are instances of this localisation; the Triassic eruptions of the southern Tirol stand in a similar relation to the Hercynian series, and the eruptions of Silurian age in Ireland and the Menez-Hom district of Brittany to a still older series. Sporadic volcanic centres, such as those of the puys of Auvergne, and multitudes of small vents, like those whose craters are still preserved in the Eifel, are characteristic of a late phase in volcanic evolution. In the Carboniferous volcanic province of Scotland Geikie has expressly distinguished a period of "puy" eruptions following that of the more important and widely-spread "plateau" out-pourings. Moreover, he has identified in Fifeshire and East Lothian the sites of many of the old vents, now marked sometimes by masses of coarse agglomerate and breccia, sometimes by a plug of rock consolidated in the throat of the old volcano.

Von Richthofen has reminded us that we are not warranted in assuming the familiar apparatus of crater and cone to be a necessary and invariable concomitant of surface volcanic action, and it may be inquired whether this phase is related to a distinct stage in the evolution of a volcanic region. It is, of course, to be borne in mind that if volcanoes of what we commonly regard as the characteristic type have been formed in the earlier stages of activity of a given period, they may often have been obliterated subsequently or concealed beneath later accumulations, and indeed the destruction of old volcanoes by a revival of explosive action is a fact of which we have direct evidence. Reviewing, however, the rather scanty information at our disposal we are inclined to regard it as more than a chance coincidence that, where the actual structure of true volcanoes has been recognised among the older formations, it is always in connection with the later maturity and gradual waning of igneous activity. The case of Monzoni, described by numerous writers, is an example, and the same rule holds as regards the Carboniferous and Permian volcanoes of Scotland, and, still earlier, in the Lower Palæozoic volcanic districts of this country. In

Anglesey and in Wicklow Sir A. Geikie has identified numerous ancient vents, apparently of late Ordovician age, filled for the most part with masses of agglomerate. In Carnarvonshire erosion has exposed the relations at a deeper level, and the sites of the old volcanoes are now marked by intrusive bosses and plugs. Here and in similar cases the scarcity of true dykes seems to be a characteristic feature.

The last-named district is sufficient in itself to illustrate many features which seem to be characteristic of an evolution of an area of igneous activity, and, in particular, it exhibits with exceptional clearness the manner in which the several stages are bound up with the local crust-movements which brought the Ordovician period to a close. The linear disposition of the old orifices of eruption is well displayed on a geological map of the district. The line runs south-westward from near Penmaenmawr far down into the Lleyn peninsula, parallel to the axes of folding, and occupying precisely the position it should have if the eruptions were a consequence of the increasing thrust from the south-east (3). It will, of course, be observed that from our present point of view the frequent linear arrangement of volcanic vents, to which we adverted at the outset, connects itself directly with the distribution of stresses in the earth's crust, visibly expressed in axes of folding, etc. Whether or not the vents are situated upon actual lines of fissure is not an essential question, and the coincidence of many lines of volcanoes with coast-lines is equally a secondary feature.

The part played by so-called "massive" or "fissure" eruptions in the volcanic history of a region is scarcely to be estimated without more precise knowledge of their nature and characteristics than we at present possess. Some great out-pourings of lava which have been regarded in this light, such as the basalts of the Snake River plains, are certainly very late occurrences. If the numerous dykes which cut the Archæan of the north-west Highlands of Scotland have been the channels of fissure-eruptions, these would seem to have been among the latest manifestations of pre-Torridon igneous activity; though, if we connect

them with the Lower Palæozoic eruptions, as apparently Bertrand would do, they assume a different significance. In the former view they afford, as Geikie has remarked, a striking parallel with the great system of Tertiary dykes in the Inner Hebrides, the south of Scotland, and the north of Ireland. These dykes, it may be observed, are basic dykes, and in well-known cases, such as the lava-plains of the Snake River and the "Deccan traps," which seem to point to the tranquil welling out of large quantities of lava, these lavas are basaltic. Something of the same tendency may be observed in some large basalt-volcanoes of the ordinary type, such as those of Hawaii. Extravasation on a "plateau" scale is, however, by no means confined to basic lavas; witness, for instance, the highly acid rhyolites of the Yellowstone Park. In explosive eruptions of the most violent kind, on the other hand, the material seems to be in many cases of intermediate (andesitic) composition, Krakatau affording a memorable example. Other intermediate lavas, such as the often-described trachytes of Auvergne, occur in dome-like masses, as if when extruded they had been too viscid to flow away from the orifices that gave vent to them. These and other well-known facts, pointing apparently to some connection between what we may term the "habit" of lavas and their petrographical nature, belong rather to the branch of the subject to which we now proceed.

Coming then to more strictly petrographical considerations, the first thing to observe is that there exists a very sharply defined geographical distribution of groups of igneous rocks differing from one another in important chemical and mineralogical characteristics. To appreciate this we must recognise a broad two-fold division of the rocks as a whole. We are accustomed to speak of acid, intermediate, and basic rocks, etc., tacitly assuming that the rocks fall roughly into a linear series, such that, as the silica-percentage varies from one extreme to the other, the percentages of the other constituents vary as functions thereof. Though this is true to a certain extent, the variations actually shown by analyses of igneous rocks indicate a much higher degree of com-

plexity. A study of the practically infinite variety of rock-types met with in nature shows that we obtain a closer approximation to the truth by assuming two linear series instead of one. Each series bridges over the interval between the extreme acid and the ultrabasic rocks, and the two lines diverge most widely in the middle. They may be represented diagramatically by two arcs meeting at either end. They are clearly traceable in either the volcanic or the plutonic division; the "dyke rocks," owing to the many peculiar types which arise as local differentiation-products, do not so readily fall into their places in this or any other scheme. To fix ideas we will take the lavas, regarding the rhyolites and the limburgites as the two extreme poles. To the one series belong the pantellarites, trachytes, phonolites and leucitophyres, nephelinites and leucitites, nepheline and leucite-basalts, and allied types; while the other includes the dacites, andesites and felspar-basalts. The leading chemical distinction lies in the behaviour of the alkalies, which in the former series increase in amount to a maximum and then fall off towards the basic end, while in the latter series they fall off steadily from the acid end to the basic. The difference is thus most marked in the intermediate members, the phonolites and allied rocks with 12 or 15 per cent. of alkalies presenting a strong contrast to the pyroxene-andesites with at most 5 or 6 per cent. This and some other differences in chemical composition naturally express themselves in the mineralogical constitution of the rocks, and most markedly so among those of mean silica-percentage. In the former series we not only find rocks composed mainly of alkali-felspars with little or no quartz, but minerals of the felspathoid group (nepheline, leucite, sodalite, etc.), often figure largely, while the characteristic ferro-magnesian minerals are alkali-pyroxenes and alkali-amphiboles in contra-distinction to the common augites and hornblendes and the widely distributed rhombic pyroxenes of the rocks of the second series.

It has been remarked above that when a region of igneous rocks belonging to one great system divides into well-marked provinces, defined by their relations to axes of

folding, these provinces often differ from one another in respect of their petrographical characteristics. This is well seen in the light of the two-fold division of igneous rocks just enunciated, and the evidence is naturally clearest in the case of the Tertiary and post-Tertiary eruptions. Iddings has already drawn attention to the remarkable geographical distribution in the New World of the two petrographical series, which he names respectively the alkali and the sub-alkali group (4). Along, and to the west of, the great continental water-shed of the two Americas the vast areas of igneous rocks belong to the sub-alkali group. On the eastern slopes of the Rocky Mountains, however, in Montana, Wyoming, Colorado, and Texas, rocks rich in alkalies appear, and farther east numerous areas characterised by rocks of the alkali group occur in Canada, the New England States, New Jersey, and Arkansas, and in Brazil, Argentina, and Paraguay. Some of these rocks, it is true, are of pre-Tertiary age, and we probably have to deal with a case of the superposition of newer upon older provinces already alluded to. Apart from this question, however, we are justified in stating summarily that, of the latest great system of igneous rocks in America, the alkali and the sub-alkali groups are developed on the Atlantic and the Pacific slopes respectively.

In Europe the distribution of the two groups is equally clear, though not to be summarised in such simple terms. Judd long ago drew attention to the strong contrast between the Tertiary igneous rocks of Bohemia and those of Hungary, divided only by the Carpathian chain. The one set belongs to the alkali, the other to the sub-alkali group. Rocks of the former group are developed along the northern border of the Alpine zone of folding, from Bohemia to France, and in the Tyrrhenian province, while the rocks of the Hungarian, Servian, and Ægean provinces are relatively poor in alkalies. The Brito-Icelandic province, partly in consequence of the very sparing development of intermediate rock-types, is less sharply characterised. The rocks as a whole seem to belong decidedly to the sub-alkali group, though they are not without anomalies.

Farther south, however, in the Cape Verde Islands, Canaries, and Azores, we find rocks of the alkali-group, and again on the Atlantic coast of Africa. Rocks of the same group are recorded in various districts on the east coast of Africa, including Madagascar, and as far north at least as Massai Land and Kilimanjaro. On the other hand, almost the whole area of the Pacific Ocean and its borders seems to be characterised by sub-alkali rocks, though a few nepheline-basalts have been noted from some of the islands. Concerning the polar oceans our information is very incomplete. The elæolite-syenites and allied rocks of Greenland show that types rich in alkalies have at one time been well represented within the Arctic circle, and the little that is known of the petrology of the far south suggests the probability that the Antarctic is also an area of alkali-rocks. Leucite-bearing rocks are found even in New South Wales, though the age of these is not known, and they recur in Java and Celebes, coming there into close proximity with andesitic and other types belonging to the great Pacific region. The leucite-bearing rocks of Trebizonde appear at present to occupy an anomalous position.

If the distribution of the two groups of rocks thus briefly outlined be laid down in greater detail on a map and distinguished by different colours, a remarkable fact becomes apparent. This is the very general correspondence of the areas of the alkali and sub-alkali groups respectively with the areas of the Atlantic and Pacific types of coast-line as defined by Suess. The one type is found around the Atlantic and part of the Indian Ocean and in the Polar basins, the other, generally speaking, around the Pacific. Whether we may have to recognise an Atlantic and a Pacific facies of eruptive rocks, corresponding with distinct phases in crust-movements of a large order, is a question which it would be premature to answer at present; but it is at least clear that the distribution, not only of igneous rocks in general, but to some extent of different petrographical groups of rocks is in some way bound up with disturbances of the earth's crust or with the forces that

produce such disturbances. What is true of the Tertiary eruptions seems to be equally true of those belonging to earlier systems. Thus, in the Caledonian region, rocks of the alkali group occur in the Norwegian and of the sub-alkali group in the British province. The point has been touched upon in an earlier communication to this Journal,[1] and need not be pursued further.

Although what has been said would suggest that petrographical provinces may to some extent have been defined as such from the beginning, their individuality has become progressively more marked as the evolution of rock types proceeded, such evolution being advanced to different stages or following different lines in the several provinces of one region. The history of any one province during its period of life is also, from the petrographical point of view, a record of progressive specialisation, resulting in increasing diversity and peculiarity of rock types. In a typical province, conceived in the sense that we have indicated, the igneous rocks belonging to the earlier stages are often characterised by considerable uniformity and simplicity. Later a greater variety may be developed, sometimes running into highly specialised types, which do not readily find a place in any classificatory scheme. This seems to be the case especially in provinces belonging to the Atlantic facies, or in other words among rocks rich in alkalies. Specialisation is accompanied by localisation, and there may arise distinct districts having peculiarities of their own. Such a general law is not to be accepted without proper qualification; in particular we must suppose that the progress of evolution may be very unequal in different cases, and may be arrested by extinction of activity when only little advanced.

For illustration we recur to the Tertiary rocks of Pacific facies in America. Iddings has compared the lavas of the Andes with those of the Great Basin, between the Rocky Mountains and the Sierra Nevada (5). The former are almost exclusively andesites and dacites; the latter include similar types but, in addition, basalts and rhyolites.

[1] "SCIENCE PROGRESS," vol. i., pp. 152-165, 1894.

Iddings interprets this wider range of variety in the northern area as indicating that evolution is there in a more advanced stage than in the south. The province of the Andes, with its still active volcanoes, is in its youth; the Great Basin, where vulcanicity seems to be practically extinct, has reached middle or old age. Even in the latter case, however, the rocks evince no very high grade of specialisation, and the same types recur in different parts of the province. A strong contrast in these respects is presented by the rocks of the alkali group on the eastern slope of the "Great Divide," where, as Iddings has shown, both specialisation and localisation are carried to a high pitch.

A similar contrast is seen on comparing the intrusive rocks developed in the same provinces. It must be remembered that the earlier identifications of the igneous rocks of the Western states often require revision. Hague and Iddings have pointed out that many of the lavas named trachyte by Zirkel in Nevada and elsewhere are more correctly designated hornblende-pyroxene-andesite, and it does not appear that true trachytes have been identified west of the Rocky Mountains. The intrusive rocks which build the well-known laccolites of the Henry Mountains in Utah and similar masses in the West Elk, Mosquito, Abajo, La Sal, and other mountain groups of the high plateaux country have also been described in various places as trachytes. Whitman Cross in a recent memoir has shown that they have no right to this title, but are in general horneblende porphrites (6). A very interesting point brought out by the author is the remarkable uniformity exhibited by the rocks of these great laccolitic intrusions over a tract extending from New Mexico northward through Utah and Colorado, and apparently at least as far as the borders of the Yellowstone Park. To this persistence of comparatively simple types of porphyrite and diorite throughout the High Plateaux and Great Basin tract are strikingly opposed the curious intrusive masses and complexes of Montana and other areas within and on the eastern edge of the Rocky Mountain belt, comprising augite and sodalite-syenites and theralites, with such peculiar modifications as the yogoite

and shonkinite of Weed and Pirsson, besides dykes of sölvsbergite (the acmite-trachyte of Wolff and Tarr), Iddings' absarokite and allied types. Apart from the significance of the laccolitic habit, of which something may be said in a future number, the petrographical uniformity of the intrusions in the former case seems to connect itself with the geotectonic structure of the country in which they occur. If the physical process, whatever their nature, which give rise to diversity of intrusive rock-types stand related in some degree to mountain-building forces of the *horizontal* kind, a smaller range of varieties is to be expected in association with the monoclinal folds, normal faults, and other evidences of *vertical* movement which characterise what American geologists have styled the Great Basin type of mountain-structure. If this be so, we should look for a greater variety of intruded rocks in the true mountain tracts farther west. Concerning Tertiary intrusions in the Sierra Nevada there seems to be little information, but in the Coast Ranges of California the intrusive rocks presumably of this age include diabase, gabbro, peridotite, pyroxenite, and other types.

If highly specialised rock-types and very local distribution of the different types may be taken as the index of advanced evolution in a petrographical province, the Tyrrhenian province has arrived at a high stage of development. The assemblage of rock-types there belongs, as already remarked, to the alkali group. It is true that andesites occur among the earlier volcanic products of the Æolian Islands and again in the Cabo de Gata district, though some of the latter have unusual characters. The later lavas, however, throughout the province, cover a wide range of types, which for the most part carry a high content of alkalies. Some, such as the remarkable acid lavas of Pantellaria and the leucite-bearing rocks of Vesuvius, are unique and of strictly limited occurrence. Among active or recently active volcanoes we find some in close proximity to one another producing widely different lavas. Thus in the Lipari group the basalts of Stromboli are contrasted with the rhyolites of Vulcano, etc., and with the rocks of the

small island Vulcanello consisting, as Bäckström has recently shown, of leucite-basanite, though quite different from the Vesuvian lavas (7). The Etna basalts have a somewhat peculiar composition. Besides the augite-trachytes, some with sodalite, near Naples, and the more singular basic variety with olivine on Ischia, many curious trachytic rocks occur at various points from Monte Amiata in Tuscany to Monte Ferru in Sardinia. The Spanish and African parts of the province have been less completely investigated, but we may recall among the Cabo de Gata rocks the peculiar glassy lava with the composition of a lamprophyre, to which Osann has given the name verite (8).

The laws governing the local distribution of the several rock-types within such a province offer a problem on which as yet little light has been thrown. Lang has attacked it from the chemical standpoint, laying special stress upon the relative proportions of the alkalies and lime in the chemical analyses of the lavas and tuffs (9). He gives reasons for believing that the numerous volcanic centres in the neighbourhood of the Bay of Naples are situated on three main lines of fissure. The rocks in each set show a considerable range of composition, but have common characteristics in the respect indicated. One fissure or set of parallel fissures, which he calls the Appenine, runs parallel with the Appenine Chain to the Alban Hills and beyond. The other two, named the Pontine and the Tyrrhenian, take more westerly courses, crossing one another obliquely in the Ponza Islands. The fissures, the existence of which is thus inferred, are of course a different order of phenomenon from the dyke-fissures to which "massive" eruptions have been ascribed. If established, their different directions and the distinctness of the associated sets of rocks point to different dates for the activity of the several fissures. Indications of such fissures, or at least of secondary directing lines of volcanic activity, are to be discerned in other provinces; for instance, as Washington has shown in the Ægean; and they have been postulated by many writers on the phenomena of vulcanicity.

One feature which can scarcely be overlooked in the

most cursory view of the distribution of igneous rocks is the frequent association of widely different types in the same district or even at the same volcanic centre. Thus, among lavas, we often find rhyolites and basalts in intimate association; among dyke-rocks, aplite and minette, or bostonite and camptonite; among intrusions of more plutonic habit, granite or granophyre and gabbro. Such cases of what may be termed paragenesis are of too frequent recurrence to be regarded as fortuitous; the members of a pair must be "complementary" rocks, connected with one another by the ties of common origin.

Several writers have endeavoured to trace some law of general application in the succession in time of different types of igneous rocks in a district or province. Besides its obvious bearing upon genetic considerations, any such established order will tend to throw light upon many points touched upon in the foregoing paragraphs, such, for instance, as the association of particular rock-types with special habits of intrusion or with certain types of volcanic eruption. That the actual facts are far from simple is evident from the very different empirical results arrived at by different geologists. Thus Bertrand, from an examination of the history of igneous activity in the European area, lays down a general law of increasing basicity in the later products of each great system of eruptions; while Geikie, dealing more especially with the British Isles, finds in general evidence of increasing acidity.

Having regard to the volcanic rocks only, a succession which holds good in numerous districts, and has often been pointed out, is what may be described as an order of increasing divergence from an initial type. For instance, the earliest lavas or fragmental outbursts being of intermediate character, say, pyroxene-andesites, succeeding eruptions have been on the one hand increasingly acid, on the other increasingly basic, terminating perhaps with rhyolites and olivine-basalts. The two lines of variation have been in a general sense concurrent, and the order of precedence between corresponding terms of the two diverging series is not always the same. This succession was

first explicitly pointed out in the Western States, and it appears to hold not only in the Great Basin and on the High Plateaux but also in Mexico. Turner has shown, however, that the volcanic rocks of the Sierra Nevada district do not conform to this order, the earliest Tertiary eruptions being of rhyolite, followed by basalt, then by andesites, and finally by a later group of basalts (10).

Reviewing the history of volcanic eruptions at various periods, we find many cases which fall under the law of increasing divergence, and the number is considerably increased if we admit the possibility of reversion at a later stage to the original type, and again if we make allowance for the partial or total suppression of one of the diverging branches by the rocks of that branch being intruded instead of extruded. For instance, the Bala volcanic series of Carnarvonshire, beginning with some rocks of andesitic composition, consists mainly of a great succession of rhyolites, no basaltic lavas being developed. The basic branch, however, is sufficiently represented by innumerable intrusive sills of diabase associated with the lavas and by laccolitic intrusions of very basic hornblendic rocks at a lower horizon. Again, Geikie has pointed out the existence at the summit of the rhyolitic group of an andesite, constituting the latest volcanic outpouring in the district, and this may perhaps be regarded as marking a new accession of the original intermediate magma. Similar examples might be multiplied, but we also find many cases which cannot, without undue forcing, be brought under the law of increasing divergence, and we are bound to admit that any generalisation taking cognisance of the observed succession of volcanic rocks only is based on a partial view of the facts.

Some years ago Brögger established clearly the order of succession of the Devonian igneous rocks, mostly of plutonic and intrusive types, in the Christiania basin. It is in general an order proceeding from more basic to more acid, beginning with olivine-gabbro-diabase and passing through progressively more acid members to granite; but the latest rocks in the district are again basic. More recently the same

author has shown that the Triassic rocks of the Monzoni district present a rather close parallel to the Norwegian series, and he gives reasons for believing that the order of increasing acidity is one of wide general application, the final reversion to basic types being also of frequent occurrence though less characteristic (11). In many districts we find among true plutonic bodies of rock and their immediate offshoots evidence of basic eruptions having been succeeded by others of more acid composition, and sometimes a series of several terms showing progressively increasing acidity. Where, however, there has been a distinct later stage characterised by dyke intrusions, the order seems to have been often, if not generally, reversed, and the more basic dykes are seen to cut the more acid. These and kindred phenomena lead to theoretical considerations which will find their place more appropriately in a future communication. In what has now been written we have confined ourselves to remarks which are the direct outcome of observation and comparison.

ALFRED HARKER.

RECENT WORK UPON VISCERAL AND ALLIED NERVES.

WITHIN the past few years our knowledge of the physiology and anatomy of the complicated tangle of nerve fibres and cells forming the sympathetic system has been making great advances; advances which are due to a very great extent to the active work of Langley and his co-workers, Dickinson and Anderson.

In the following account of our present knowledge of this subject I will first confine myself to the question of efferent fibres, leaving the discussion of the afferent fibres, upon which our knowledge is much scantier, for a later paper. Our proper appreciation of the true anatomical and physiological status of the sympathetic system may be said to date from 1885 when Gaskell's important paper on visceral innervation appeared in the *Journal of Physiology*.

For the purposes of this paper I have not referred back to earlier work than this, except in a few instances where it was necessary to make the account a little more complete. In most cases, however, the papers utilised have been published within the past five years. The whole has been divided up into sections, each giving an account for the different organs, and I have placed that for the pilo-motor nerves first as giving in many ways a more complete picture than any other, of the general arrangement of fibres and cells in the sympathetic system.

PHILO-MOTOR NERVES.

The nerves which Langley and Sherrington have designated "pilo-motor," and which on stimulation cause contraction of the erectores pilorum and erection of the hairs, have been shown to form a constituent part of the sympathetic system.

Schiff[1] showed that electrical stimulation of the spinal

[1] Quoted by Langley, *Journ. of Physiol.*, vol. xv., p. 241, 1894.

cord caused erection of hairs in the tail, but that this effect disappeared after section of both lumbar sympathetic cords. Independently of this, and of one another, Langley[1] discovered that stimulation of the lumbar sympathetic in the cat caused erection of hairs, and Sherrington that stimulation of the cervical sympathetic in the monkey produced a similar effect. Starting with this as a basis Langley[2] has thoroughly worked out the course and distribution of these fibres, employing his results as a general indication of the arrangement of fibres of the sympathetic system.

He has shown that in the cat they arise from the cord in the anterior roots from the fourth thoracic to the third lumbar inclusive. In rare cases some were also found in the third thoracic and at times in the fourth lumbar, but, probably, only in the latter nerve, in those cats in which the arrangement of the lumbo-sacral plexus is posterior. These fibres leave the mixed nerve in its white ramus communicans and run to the corresponding ganglion, thus entering the sympathetic system. From these ganglia they may run upwards or downwards and ultimately leave in the grey rami to the various nerves and so reach the skin areas which they supply.

In a typical nerve all the pilo-motor fibres joining by its grey ramus pass into the posterior primary division of the nerve and are thus distributed to serial areas of the skin of the back which do not to any extent overlap one another.

This course was further examined to determine whether any nerve cells were interpolated on it. The method employed was that previously described by Langley and Dickinson,[3] who found that a solution of nicotine exerted a specific paralysing action on ganglion cells whether injected into the animal or applied locally, in 1 per cent. solutions, to the ganglion. After painting a ganglion with this solution he found that stimulation of the pilo-motor fibres running to this ganglion to leave it by its grey

[1] *Journ. of Physiol.*, vol. xii., p. 278, 1891.

[2] *Ibid.*, vol. xv., p. 176, 1894.

[3] *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889, and vol. xlvii., p. 379, 1889-90; *Journ. Physiol.*, vol. xi., p. 265, 1890.

ramus, almost without exception, produced no effect, though stimulation of the grey ramus produced the usual erection of hairs over its especial area of supply. Each pilo-motor fibre, therefore, leaves the cord in an anterior root and passes by the white ramus communicans of that nerve to the sympathetic system, and after a longer or shorter course ends in connection with a cell or cells in a sympathetic ganglion of the lateral chain. From this the impulses are carried by a fibre or fibres to the grey rami, and thence to their skin distribution. The ultimate distribution of the fibres in a white ramus usually does not in any way correspond to the distribution of the grey ramus running from that ganglion. Thus, for example, stimulation of the anterior roots of the eleventh thoracic nerves after previous ligature and section produced erection of a longish strip of hairs in the lumbar region, whilst stimulation of the grey ramus of that nerve produced energetic erection of hairs in a short strip a little distance above the long strip, and separated from it by a quiescent region. The areas supplied by successive anterior roots are found to form successive strips which, however, frequently overlap one another to a considerable extent. Langley[1] found that stimulation of an anterior root with weak shocks produced an erection of hairs supplied by all the fibres issuing by that root. Then if the strength of the stimuli be considerably increased in addition to the first effect, an erection of hairs in a narrow strip supplied by the grey ramus running to that nerve is now produced. The first effect is obliterated on paralysing the ganglion cells by injection of nicotine whilst the latter effect is of course unaffected.

In the monkey, Sherrington showed that the pilo-motor fibres found in the cervical sympathetic left the cord by the second to the sixth thoracic nerves, and had ganglion cells upon their course in the superior cervical ganglion. Thence they are distributed to the hair on the forehead, front of scalp, temple, cheek and the upper part of the whisker.

[1] *Loc. cit.*, p. 203.

In the cat, Langley found that the similar fibres leave the cord from the fourth to the seventh thoracic nerves—on rare occasions by the third as well—and thus reach the superior cervical ganglion, where nerve cells are interpolated on their course. The grey rami to the first, second and from the ganglion and supply two regions—(i.) a "face third cervical nerves and the cranial rami carry the fibres area," between the eye and the ear, supplied by the latter; and (ii.) a dorsal strip extending from just behind the anterior level of the ears to, as a rule, some point over the fourth vertebræ.

The next set of nerve fibres have their cells in the ganglion stellatum. These leave the cord in the fifth to eighth thoracic nerves, and from the ganglion are distributed by a vertebral ramus to the third to eighth cervical nerves and supply a dorsal strip extending from the fourth cervical vertebra to the front of the third thoracic vertebra. This strip is narrow above and broadens out below. The ganglion stellatum also sends pilo-motor fibres by its grey rami to the first, second, third and fourth thoracic nerves. These supply areas roughly corresponding to one vertebra each, and thus extend from the third to the seventh or even eighth thoracic vertebra.

For the remaining ganglia of the chain, the fibres leave the cord from the seventh thoracic to the third or fourth lumbar nerve inclusive. The third is usually the last, and supplies fibres to the parts from the anus to the tip of the tail. As a rule, the nerve cells for these pilo-motor fibres are in the ganglia, from which they are given off to the spinal nerves, though occasionally in the lumbar region, they are placed in the ganglion immediately above. Each grey ramus supplies the skin over about one vertebra. Thus the grey ramus to the fourth lumbar nerve supplies the hairs over the seventh lumbar vertebra and sacrum. There is a curious gap in the distribution to grey rami, for usually that to the sixth lumbar nerve contains no hair fibres. There is, however, no gap in the skin distribution, and the first sacral grey ramus follows the lowest effective lumbar ramus. The first effective ramus below the in-

effective lumbar ramus or rami supplies a strip of skin immediately below the sacrum.

The second sacral supplies the hairs dorsal to the anus; the third, those about one inch below the anus; and the coccygeal, the remainder to the tip of the tail.

Now, by a comparison of the full areas supplied by the anterior spinal roots with the areas of the grey rami, the accurate connection of any anterior root with the ganglia, or conversely of any ganglion with the anterior roots, can be determined; and Langley, in his later paper, gives a series of tables[1] in which this has been done.

In a few experiments on the dog, Langley found that the general arrangement of these fibres is the same as in the cat.

Where, as is usually the case in tracing the course of these sympathetic fibres, we find that their path is made up of two segments, each consisting of a nerve cell and its fibre, the upper fibre whose cell is placed in the spinal cord and which terminates in dendrites in one or other of the ganglia of the system is termed by Langley the præ-ganglionic fibre. The other fibre, whose cell is placed in the ganglion and whose fibre runs, as a rule, to the nerve-ending in the organ, he terms the post-ganglionic.

In considering, moreover, the origin of the different fibres in the lumbar region, there are other points of nomenclature adopted by Langley which are of great importance. As the number of thoracic and lumbar nerves is very variable, and as the first sacral is a nerve which is always readily distinguished from all others, he starts with this as his fixed nerve. The immediately preceding seven nerves are called the first, second, etc., lumbar nerves successively.[2] If there is another lumbar nerve above that, it is termed the extra lumbar. Sometimes, moreover, the seventh nerve above the first sacral has a small rib, but this he still terms the first lumbar nerve.

Langley[3] also describes the lumbo-sacral plexus of the

[1] *Loc. cit.*, pp. 220, *et seq.*

[2] See Langley, *Journ. of Physiol.*, vol. xvii., p. 297, 1894-5.

[3] *Loc. cit.*, p. 296.

cat as presenting several variations. These he divides into three chief groups called respectively anterior, median, and posterior. "The simplest method of distinguishing these classes is to note the relative size of the strands to the sciatic furnished respectively by the sixth lumbar and by the upper branch of the first sacral. If the former is distinctly larger than the latter, the plexus belongs to the anterior class; if the two are of about the same size, the plexus is median; if the strand from the first sacral is distinctly larger than that from the sixth lumbar, the plexus is of the posterior class."

VASO-MOTOR NERVES.

Gaskell,[1] in his important paper upon visceral and vascular nerves, deals with the question of the course and distribution of the two sets of vaso-motor nerves. The method he employed was to a large extent an anatomical one. He showed that the visceral fibres present in any root may all be traced into the white ramus communicans of that root, because their transverse diameter is much smaller than the average diameter of the ordinary sensory and motor fibres of the two roots. He concludes that vaso-constrictor nerves for all parts of the body are restricted to the anterior roots of the spinal nerves between the second thoracic and fourth lumbar inclusive, whence they pass as medullated nerves to the ganglia of the main sympathetic chain, from which they issue as non-medullated nerves and pass to their destination. For vaso-dilator nerves, he shows that some leave by the cervico-cranial and sacral sets of visceral nerves; but whether there are more from other roots he does not decide.

To the Trunk and Limbs.—By recording plethysmographically the variations in volume of the limbs and the general blood pressure simultaneously, Bradford and Bayliss[2] have examined the origin of the constrictor nerves to the limbs. For the fore-limb in the dog, they find constrictor

[1] *Journ. of Physiol.*, vol. vii., p. 1, 1885-6.
[2] *Ibid.*, vol. xvi., p. 10, 1894.

fibres issuing by the third to eleventh thoracic inclusive, but chiefly by the fifth to ninth inclusive. For the hind limb, from the eleventh thoracic to third lumbar inclusive, mainly however in the twelfth thoracic to second lumbar inclusive.

Langley[1] finds that the fibres for the upper limb terminate in the cells of the ganglion-stellatum; those for the hind limb in cells in the sixth and seventh lumbar and first sacral ganglia. The fibres issuing from these cells run chiefly into the corresponding grey ramus, but in a few cases may run down the sympathetic chain and issue by the grey ramus of the next ganglion. Langley,[2] in a later paper on the constrictor supply to feet of the cat, shows that they leave the cord in the fourth to ninth thoracic nerves inclusive for the fore foot; and to the hind foot in the twelfth thoracic to third lumbar nerves with an anterior plexus, or in the twelfth thoracic to fourth lumbar with a posterior plexus. On the whole, the two results agree when we remember that Bayliss and Bradford's experiments were performed upon the dog, and involved the larger part of the limb, and that Langley's observations were made on the cat, and were restricted to the vessels of the feet.

E. Cyon,[3] in 1868, by studying the effects upon the temperature of the limb after section of the sympathetic cord in various positions, and of the lower cervical and upper dorsal rootlets, concluded that the vaso-constrictor fibres for the upper limb leave the cord through the mid-dorsal roots, thence travel to the ganglion-stellatum, and so by its rami reach the cords of the brachial plexus.

With regard to the vaso-motor fibres to the trunk, Langley[4] finds that, in the main, they are the same as the origin of the pilo-motor fibres, though their distribution for any particular ramus is as a rule rather more extended than that of the latter from the same ramus.

[1] *Journ. of Physiol.*, vol. xii., p. 373, 1891.
[2] *Ibid.*, vol. xvii., p. 307, 1894-5.
[3] *Leip. Ber.*, vol. xx., p. 73, 1868.
[4] *Loc. cit.*, p. 312.

The pre-ganglionic vaso-motor nerves to the tail[1] leave the cord by the third and fourth lumbar nerves and to a less extent by the second lumbar. By nicotine it is shown that these fibres are connected with cells in the coccygeal ganglia.

To the Head.—The pre-ganglionic fibres constricting the vessels of the head,[2] in the cat and dog, leave in the first to fifth thoracic anterior roots inclusive, but chiefly in the second, third and fourth. They terminate in cells in the superior cervical ganglion.[3] Certain fibres causing dilatation of the vessels in the gums and lips in the dog, have also been shown by Langley and Dickinson to be connected with cells in the superior cervical ganglion.[4]

To the Brain.—Roy and Sherrington,[5] in a paper dealing with the general physics of the circulation in the brain, were unable to gain any satisfactory evidence of vaso-motor fibres to the cerebral vessels in the nerves of the neck, "and that therefore there is no evidence of their existence outside the cerebro-spinal canal". Bayliss and Hill[6] have also carried out many experiments with the aim of determining the presence of these vaso-motor fibres, but again with negative results.

The course of efferent fibres from the cord is almost universally considered as through the anterior roots, and so general is this that any statement of the presence of efferent fibres in the posterior roots should be most critically examined. In 1876 Stricker[7] described his experiments and results upon the vascular nerves in the sciatic. His method was by thermometric observation of the foot after section or stimulation of the nerves in different parts of their course. He describes the posterior roots of the fourth and fifth lumbar nerves of the dog as always containing vaso-dilator

[1] Langley, *loc. cit.*, p. 311.
[2] Langley, *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.
[3] Langley and Dickinson, *Proc. Roy. Soc.*, vol. xlvii., p. 379, 1889-90.
[4] See also Langley, *Journ. of Physiol.*, vol. ii., p. 146, 1890.
[5] *Journ. of Physiol.*, vol. xi., p. 85, 1890.
[6] *Ibid.*, vol. xviii., p. 334, 1895.
[7] *Sitz. d. k. Ak. d. Wiss. Wien*, vol. lxxiv., iii., p. 173, 1876.

fibres which run directly into the sciatic. The constrictor fibres are situated in the lower thoracic and upper lumbar and pass through the sympathetic chain. The presence of these fibres in the posterior roots has given rise to much discussion. Stricker's results were confirmed by Gärtner, but denied by Vulpian, Cossy, etc. Of recent workers Morat[1] cannot confirm the presence of these fibres, but on the other hand Hasterlik and Biedl[2] confirm Stricker's experiments. In this connection we find anatomical evidence of the presence of fibres in the posterior roots which have the characters which are usually regarded as typical of efferent fibres. Ramon-y-Cayal[3] describes fibres passing through the posterior roots and without branching going straight to the anterior horn, where they end in nerve-cells. v. Lenhossek[4] also describes similar fibres and cells—the fibres passing though the posterior root ganglion without becoming connected with cells in that ganglion. Lastly v. Gehuchten[5] finds similar cells in his examination of the spinal cord of the fowl at early stages of development.

Werziloff[6] has recently published further experiments in this direction. He employed for his experiments large dogs which were curarised and under chloroform. His methods were two in number; either to examine temperature changes as each posterior root was cut, or to place the hinder leg in a plethysmograph and so obtain tracings of the changes in volume. He describes very positive evidence of vaso-dilator fibres in the sixth and seventh lumbar, and first sacral posterior roots for the foot and similar fibres, though less numerous, in the fourth and fifth lumbar for the upper part of the leg and lower part of the thigh.

Gaskell[7] especially examined the posterior roots of the first, second and third sacral for the presence of vaso-dilator

[1] *Arch. de Physiol.*, vol. xxiv., p. 689, 1892.
[2] *Wiener. klin. Wochenschr.*, p. 43, 1893.
[3] *Anat. Anz.*, vol. v., p. 112, 1890.
[4] *Ibid.*, p. 360, 1890.
[5] *Ibid.*, vol. viii., p. 215, 1893.
[6] *Centr. f. Physiol.*, vol. x., p. 194, 1896.
[7] *Journ. of Physiol.*, vol. viii., 1887; *Proc. Physiol. Soc.*, p. 4.

fibres running into the nervi erigentes, but never found them (rabbits). They always passed through the second and third anterior roots.

To the lungs.—Bradford and Dean[1] describe vaso-constrictor fibres to the pulmonary vessels as occurring in the anterior roots of the third, fourth and fifth thoracic nerves and to a less extent in the sixth and seventh. They experimented upon dogs, taking simultaneous tracings of the variations of pressure in the pulmonary artery and carotid. Their results have been confirmed by François Franck.[2] He criticised their method as not being the best, and liable to introduce factors difficult to interpret. He therefore took simultaneous pressure tracings of the pulmonary artery and left auricle, and required as a test for constriction of the pulmonary artery a simultaneous rise of pressure in the artery, with a fall in the auricular pressure. In this way he finds that the constrictors are chiefly placed in the second and third thoracic nerves, and that none are found below the fifth and sixth.

With regard to the origin and distribution of the vascular nerves to other organs, it will be more convenient to state what is known of them when discussing the general nerve supply of each organ. In this way we shall save repetition. for the origin of the vascular nerves is the same, as a rule, as that of the visceral fibres.

THE CARDIAC NERVES.

The *accelerator* nerves, as Langley[3] has shown, leave the cord chiefly by the second and third thoracic roots, to a less extent in the fourth thoracic, and to a much slighter extent in the first and fifth thoracic. It is indicated by a few experiments, though not conclusively proved, that the cells on the course of these fibres lie in the ganglion stellatum and inferior cervical ganglion. The experiments were carried out on cats. The spinal origin of these fibres is confirmed for the dog by Bayliss and Starling.[4]

[1] *Journ. of Physiol.*, vol. xvi., p. 34, 1894.
[2] *Arch. de Physiol.*, vol. xxvii., pp. 744 and 816, 1895.
[3] *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.
[4] *Journ. Physiol.*, vol. xvii., p. 126, 1894.

The *inhibitory* fibres of the vagus have also had their origin and cell-connections investigated. Grossmann[1] examined the rootlets of the ninth, tenth and eleventh cranial nerves to determine in which of these rootlets the inhibitory fibres left the medulla. For purposes of reference he divides the rootlets into the three groups as they are anatomically arranged; these groups he speaks of as group (*a*), (*b*) and (*c*) respectively. The fibres of group (*a*) correspond fairly well, though by no means entirely, with the fibres forming the glosso-pharyngeal, group (*b*) with the vagus, and group (*c*) with the medullary origin of the spinal accessory. He examined each of these rootlets as they leave the medulla, employing rabbits as the animals experimented upon, for cardio-inhibitory nerves by unipolar stimulation of each rootlet immediately as it arose from the medulla, after cutting it through close to its origin or after tearing it from the medulla. He found them in the lower two or three rootlets of group (*b*) and the upper rootlet of group (*a*). F. Vas[2] has also examined these same rootlets in the skull cavity for their effect upon the heart. He tears through the rootlets and notes the effect upon the heart and upon the blood pressure. He does not find any cardiac nerves in the accessory rootlets. With regard to the further connections of these fibres Gaskell[3] showed that in the crocodile and alligator, by the degeneration method, these fibres had no connection with cells in the ganglion trunci, but were continued straight down as medullated fibres to their termination in the heart substance, where their endings were probably in relation with some of the cardiac ganglion cells. This connection of the fibres with intrinsic cardiac ganglia is shown by the action of nicotine applied locally to the heart.[4] After the application of nicotine the heart can no longer be inhibited by stimulation of the vagus in the neck, though it can if the fibres in the substance of the heart be stimulated. The vagus fibres

[1] *Pflüger's Archiv*, vol. lix., p. 1, 1894.
[2] *Ungar Arch. f. Med.*, iii., 1894.
[3] *Journ. of Physiol.*, vol. vii., p. 22 *et seq.*, 1885-6.
[4] See Langley and Dickinson, *Journ. of Phys.*, vol. xi., p. 279, 1890.

therefore from their medullary origin to their termination in the intrinsic ganglia form the præ-ganglionic fibres, from the ganglion cells to the heart muscle terminals the post-ganglionic. This double segmentation is also confirmed by a degeneration method by Nikolajew.[1]

INNERVATION OF THE MUSCULAR WALLS OF THE ALIMENTARY CANAL.

Œsophagus. — It has long been known that peristaltic contractions of the œsophagus may be produced by stimulation of the vagus either in the neck or thorax. Gaskell[2] investigated the function and course of these fibres, choosing crocodiles and alligators for his experiments, because in these animals the two vagal ganglia, ganglion jugulare and ganglion trunci, are separated by the whole of the cervical portion of the vagus. Stimulation of the nerve in the crocodile either above or below the ganglion trunci produced a strong peristaltic contraction of the œsophagus extending through both the cervical and thoracic portions and ending in a contraction of the stomach. In the alligator the course of the fibres is a little different, those for the thoracic portion running as in the crocodile, whilst the fibres for the cervical portion "pass directly to it probably by way of the large conjoint vagus and glossopharyngeal ganglion and the pharyngo-laryngeal nerve.

The presence of nerve cells on the course of these fibres was next investigated by removal of a piece of the vagus in the neck and observation of the effects of stimulation of the nerve above and below the ganglion trunci. It was thus proved that the motor fibres for the thoracic portion of the œsophagus have nerve cells interposed upon their course, and that these cells are situated in the ganglion trunci. In the crocodile the fibres for the cervical portion of the œsophagus pass through the ganglion without coming into connection with the nerve cells. These fibres above the ganglion are fine medullated fibres, whereas below the ganglion they are found to be non-medullated.

[1] *Arch. f.* (*Anat. u.*) *Physiol.*, suppl., p. 67, 1893.
[2] *Journ. of Physiol.*, vol. vii., p. 19, 1886.

Kreidl[1] has examined the roots of the glossopharyngeal, vagus and accessory at their exit from the medulla to determine in which rootlets these fibres leave the central nervous system. These roots are described by Grossmann[2] as arranged in three groups, which, for convenience of description, he speaks of as group (*a*), group (*b*), and group (*c*). Group (*a*) corresponds chiefly to the glossopharyngeal, (*b*) to the vagus, and (*c*) to the spinal accessory.

Kreidl's method consists in dividing one or more of these roots at their exit from the medulla without anæsthetics and shortly after they have been given a meal consisting of green food-stuffs. The animals (rabbits) are then allowed to recover and given a meal of carrots. In those experiments in which the roots of either groups (*b*) or (*c*) had been divided no paralysis of the œsophagus was observed, but where group (*a*) had been divided the animal soon ceased to eat and the œsophagus was found full of food. This result was constant in over thirty rabbits. He further shows that section of the glossopharyngeal immediately after it leaves the cranium has no influence over the result, and that consequently the fibres after passing through the roots of group (*a*) pass directly into the vagus.

Steinach[3] states that in the frog not only does the vagus contain motor fibres for the œsophagus, but that similar ones are present in the *posterior* roots of the second and third nerves.

Réthi[4] by stimulation of the peripheral end of these roots concludes that the fibres for the tensor palati leave in the motor root of the fifth, for the stylo-pharyngens in group (*a*) and for the constrictors of the pharynx, the levator-palati, the palato-pharyngeus, and the palato-glossus in group (*b*).

Stomach.—In a paper upon the peristaltic contraction of the stomach and intestines, which contains an account of

[1] *Pflüger's Archiv*, vol. lix., p. 9, 1895.
[2] *Ibid.*, p. 1, 1895.
[3] *Ibid.*, vol. lx., p. 593, 1895.
[4] *Sitz. d. k. Ak. Wien*, vol. ci., Abt. iii., p. 381, 1892.

the earlier literature, Houckgeest[1] confirms and extends previous observations upon the innervation of the stomach. He concludes that both right and left vagi contain fibres stimulation of which leads to an increase in the movements of the stomach, and that the two splanchnics contain inhibitory fibres to the stomach muscles.

Openchowski[2] in two papers describes the results of his experiments upon the central and peripheral innervation of the stomach. His method consists of the introduction of a sound carrying an elastic bag into the stomach. The bag is brought into different positions in the pylorus, the cardiac orifice or the cavity of the stomach, and by being connected with a recording tambour tracings of the movements of the different parts may be obtained. He concludes that the different parts possess a power of rhythmic contraction which, however, is modified by nervous impulses reaching it from the brain or cord. For the cardiac orifice there are two sets of fibres, one set opening the other closing the orifice. The latter he describes as passing from a centre in the region of the posterior corpus quadrigeminum by two different paths. The first and chief one is *via* the vagus, especially the left, the second down the cord and out by the anterior roots of the fifth to eighth thoracic nerves inclusive, and thence by the splanchnics to the stomach. The fibres, stimulation of which leads to the opening of the cardia, he describes as passing either down the vagus or along the cord, to issue by the upper thoracic nerves as low as the fifth and thence by the splanchnics, especially the smaller. For the pyloric orifice the constrictor fibres pass along the vagus and the dilator fibres pass down the cord and leave it in the anterior roots of the thoracic nerves above the tenth. He states that, in the rabbit, there are more excito-motor fibres than inhibitory in the splanchnic, whereas in the dog the reverse is the case.

[1] *Pflüger's Archiv*, vol. vi., p. 266, 1872.

[2] *Arch. f. Anat. u. Physiol.*, p, 549, 1889, and *Centralblatt f. Physiol.*, vol. iii., p. 1, 1889.

Langley and Dickinson[1] found that in the dog or cat stimulation of the vagus caused movement of the stomach and stimulation of the splanchnic inhibited that movement.

Oser[2] examined the innervation of the pylorus by observation of its condition through an opening in the duodenum either by means of a cylindrical rubber bag passing through it, or by simply passing a finger through it and noting the resistance offered. He found that stimulation of the vagus markedly increased that resistance and stimulation of the splanchnic had the reverse effect. By introducing a sound and filling the stomach with warm saline solution after the duodenum had been occluded by a ligature below the pylorus he showed that stimulation of the vagus produced a marked contraction which was followed after the cessation of the stimulus by a relaxation to a greater extent than before stimulation. Stimulation of the splanchnic produced cessation of any irregular rhythmic contractions that might have been present, accompanied by a relaxation. On cessation of the stimulation, the tonic contraction increased and was accompanied by an unusually active rhythm which however is easily inhibited by renewed splanchnic stimulation. His experiments were carried out upon dogs.

Morat[3] investigated the movements of the stomach by introducing a sound carrying a thin-walled bag into the empty stomach. The bag can then be distended to a certain extent and registers the movement of the stomach-wall. He describes a marked rhythm which varies very much in different cases, but increasing in rate, in force and in tone, on stimulation of the peripheral cut end of either vagus. Stimulation of the splanchnic brings about the reverse effect, *viz.*, a diminution in the amount of tone, and a fall in the rate and force of the rhythm. He moreover found evidence of muscular inhibitory fibres in the vagus, for he found that stimulation of the central end of one divided vagus, the opposite being intact, produced a dilation of the organ which dilatation was not produced if the

[1] *Proc. R. S.*, vol. xlvi., p. 423, 1889.
[2] *Zeitschr. f. klin. Med.*, vol. xx., p. 285, 1892.
[3] *Arch. de. Physiol.*, vol. xxv., p. 142, 1893.

opposite vagus was cut. Doyon[1] confirms this result and adduces further evidence of the presence of these inhibitory fibres in the vagus, for he finds that after the injection of pilocarpine the first effect of stimulation of the vagus is to produce dilatation which is later followed by the usual contraction. The injection of strychnine in suitable doses gives practically the same result.

Contejean[2] experimenting on frogs and toads describes the vagus as carrying motor fibres to the general stomach wall and to the cardiac and pyloric sphincters, and in addition fibres inhibiting movements of the sphincters. By a weak stimulation inhibitory effects are produced; with strong stimulation energetic contraction of the cardia and pylorus, then of the longitudinal fibres and finally peristalsis; stimulation of the sympathetic, or better of the cœliac plexus, leads to contraction of the circular fibres, but not peristalsis. If in a curarised frog water be placed in the mouth after both vagi are cut this is not driven into the stomach, and the cardiac orifice shows marked rhythmic contractions, thus illustrating the absence of the usual inhibitory effects. If, on the other hand, both vagi be cut in a non-curarised frog the results obtained are due to a failure of the usual motor effects, *e.g.*, air taken into the mouth is driven into the stomach as well as into the lungs.

Doyon[3] has examined the innervation of similar parts in pigeons and fowls. The crop is a part of the œsophagus and is innervated in a similar manner to it. The gizzard and proventriculus show rhythmic contractions which are increased in number and in rate by vagal stimulation and also increased in tonus. Stimulation of the splanchnic arrests rhythmic movements if these be present, but if the organs be at rest it may produce a single contraction. Stimulation of the central end of the vagus the other being intact causes relaxation of the gizzard and proventriculus, an effect which is abolished by section of the opposite vagus. Pilocarpine

[1] *Arch de Physiol.*, vol. xxvii., p. 374, 1895.

[2] *Comp. Rend.*, vol. cxiii., p. 150, 1891, and *Arch. de Physiol.*, vol. xxiv., p. 640, 1892.

[3] *Arch. de Physiol.*, vol. xxvi., p. 887, 1894.

causes contraction of the crop, gizzard and proventriculus, and if while these parts are thus firmly contracted the vagus be stimulated, a dilatation of the gizzard and proventriculus is produced. In these two ways then the presence of inhibitory fibres in the vagus is demonstrated.

With regard to the presence of nerve cells upon the course of these fibres, Gaskell[1] showed in his experiments upon alligators and crocodiles that the fibres for the stomach contained in the vagus were connected with nerve cells in the ganglion trunci vagi, and that here too they became non-medullated.

Langley and Dickinson[2] have further shown that the inhibitory fibres contained in the splanchnic terminate in cells in the cœliac ganglion, and that the motor fibres of the vagus do not become connected with cells in the solar plexus or its immediate offshoots. After painting the cœliac plexus with nicotine the rhythmic movements of the stomach are greatly increased, and stimulation of the splanchnic no longer interferes with that rhythm. Steinach[3] describes motor fibres for the stomach of the frog in the vagus, and also in the posterior roots of the third and fourth spinal nerves.

Small Intestine.—It has been commonly stated that the arrangement of the double nerve-supply of the small intestine is that the one set, vagus fibres, cause contraction of the circular and inhibition of the longitudinal fibres, the second set, splanchnic fibres, cause contraction of the longitudinal and inhibition of the circular fibres. The view that the general function of the vagus is excito-motor and of the splanchnic inhibitory appears however to be the one which results from the experiments of most later observers, though at times the splanchnic may give rise to contractions but not of the ordinary peristaltic character. These irregular contractions caused by stimulation of the splanchnic may well be due to secondary effects brought about by the constricting influence which the nerve exerts over the blood-vessels.

Houckgeest[4] in his experiments upon peristalsis con-

[1] *Loc. cit.* [2] *Loc. cit.* [3] *Loc. cit.* [4] *Loc. cit.*

firms the fact that vagus stimulation increases the peristaltic contractions more especially after previous section of the two splanchnics. That the splanchnic contained inhibitory fibres he considered was to be deduced from the marked increase in peristaltic activity consequent upon their section.

Langley and Dickinson[1] obtained marked increase of peristaltic movements on stimulation of the vagus, an increase which was quickly inhibited by stimulation of the splanchnic. Pal and Berggrün[2] showed that the effect of the vagus could be very largely increased if before stimulation the cord be cut in the neck or a transverse section of the brain be made at the pulvinar or anterior third of the optic thalamus, and concluded that inhibitory fibres passed through the parts cut. Pal[3] showed that many of the irregular results obtained in experiments upon the muscular movements of the intestines were due to their exposure to the air. He observed the movements through the abdominal wall after this had been shaved, and found that on stopping artificial respiration in curarised dogs or rabbits these movements were greatly increased, an increase which was not abolished by section of both vagi, though the contractions could be made much more vigorous by stimulation of either vagus. On opening the abdomen the movements quickly ceased, and a second stimulation of the vagus produced either no effect or only a weak contraction. Moreover on now stopping artificial respiration the peristalsis which was so marked when the abdomen was intact no longer occurred. He also adduces experiments[4] to show that in addition to the ordinary splanchnic centre there is another placed lower down in the cord which inhibits peristalsis. His statement is general, not limited to the lower part of the small intestine or to the large intestine. Jacobi[5] examined the movements of the intestine in animals in which the intestines were exposed under warm

[1] *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889.
[2] *Wien med. Jahrb.*, p. 434, 1888.
[3] *Arb. a. d. Inst. f. alg. u. exper. Path. Wien*, p. 31, 1890.
[4] *Wiener. Klin. Wochenschr.*, pp. 199, 521, 1895.
[5] *Arch. f. exp. Path. u. Pharm.*, vol. xxix., p. 171, 1892.

saline solution, and confirmed the ordinary effects of vagus and splanchnic, finding, however, that the vagi usually had unequal actions, sometimes the left sometimes the right producing greater peristalsis. Bechterew and Mislawski[1] experimented with the object of determining the roots by which the fibres in the splanchnic innervating the small intestine left the cord. They found them in the anterior roots of the sixth thoracic to first lumbar inclusive.

Langley and Dickinson[2] showed that painting the superior mesenteric ganglion with nicotine abolished the effect of splanchnic stimulation, and that the motor fibres of the vagus do not end in cells of the solar plexus. Further, Gaskell[3] showed by the method of degeneration that in all probability the motor fibres of the vagus are connected with cells in the ganglion trunci vagi.

We may therefore sum up our knowledge of the muscular innervation of the small intestine in the following way: (1) A set of five medullated fibres leave the medulla in the vagal rootlets, are connected with cells in the ganglion trunci, and then continue as non-medullated fibres straight to the intestinal walls, passing through the solar plexus but not being connected with cells in that plexus. Stimulation of this set causes contraction of both the longitudinal and circular coats. (2) A set of fine medullated fibres arise from the cord, leave by the anterior roots from the sixth thoracic to the first lumbar inclusive, pass through the lateral chain of ganglia and are connected with cells placed chiefly in the superior mesenteric ganglia. Thence they are traced as fine non-medullated fibres to the muscular coats. Stimulation of these fibres causes inhibition of any peristallic movements that may be present. At times stimulation has been noted to cause an isolated contraction, often local and of a non-peristallic nature, a contraction which may most reasonably be accounted for as an effect secondary to the contraction of blood-vessels, simultaneously caused by the stimulation.

[1] *Arch. f.* (*Anat. u.*) *Phys.*, suppl., p. 243, 1889.
[2] *Loc. cit.*
[3] *Journ. of Phys.*, vol. vii., p. 19, 1886.

According to Steinach, the upper part of the small intestine of the frog receives motor fibres through the posterior roots of the fourth and fifth nerves, the lower part through the fifth and sixth.

Vaso-motor Nerves to the Intestines.—The course of the vaso-constrictors to the stomach and small intestine has long been known to be by the splanchnics. Langley and Dickinson[1] showed that their course was interrupted by nerve cells which were placed in the cœliac or superior mesenteric ganglia. Painting the ganglia with nicotine abolishes the usual effect on the blood pressure, of stimulation of the splanchnic. The local application of nicotine to the ganglia causes first a rise in blood pressure, stimulating action on the nerve cells, followed by a marked fall as the cells become paralysed. In a recent paper, Langley[2] gives further evidence of the position of the cells on the course of the vascular fibres to the intestine. After a sufficient dose of nicotine, the marked rise in blood-pressure consequent on stimulation of the splanchnic is abolished, but stimulation of the nerves leaving the solar plexus can still produce the usual rise in blood-pressure. He concludes that there is one, and only one, cell station on any vaso-constrictor nerve. Contejean,[3] for the frog, describes both vaso-dilators and constrictors as occurring in the vagus, the dilators being present to the greatest extent. The main number of the constrictors reach the organ by the sympathetic chain.[4] Hallion and François Franck[5] have recently published some experiments upon the origin and course of these nerves. Their method is a plethysmographic one and consists in enclosing one or more loops of the intestine in a glass vessel in which it is covered by warm saline solution. The upper orifice is closed by an air-tight lid, and changes in pressure of the air imprisoned over the salt solution are recorded by means of a sensitive

[1] *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889.
[2] *Journ. of Physiol.*, vol. xx., p. 223, 1896.
[3] *Comp. rend.*, vol. cxiii., p. 150, 1891.
[4] *Arch. de Physiol.*, vol. xxiv., p. 640, 1892.
[5] *Ibid.*, vol. xxviii., pp. 478 and 493, 1896.

tambour. Simultaneous blood-pressure tracings and plethysmographic tracings of other parts, spleen, kidney, etc., were also taken. They describe the vaso-constrictors as leaving the cord from the fifth thoracic downwards. The upper of these supply the upper part of the intestine, duodenum and jejunum, the lower part supplying the ileum and colon. Stimulation of the eleventh, twelfth, and thirteenth thoracic, and first and second lumbar white rami causes a constriction soon followed by a marked dilation of the vessel accompanied by a fall in blood pressure. These roots, therefore, contain the chief vaso-dilator fibres.

Lower Part of Intestinal Canal.—Fellner,[1] in working upon the innervation of the rectum, supports v. Basch's theory that where there is an organ with double muscular wall and double nerve supply, the one set of nerve fibres causes contraction of one muscular layer and inhibition of the second, whilst the other set of nerve fibres exerts the reverse effect. In accordance with this Fellner describes that in the dog stimulation of the nervus erigens causes contraction of the longitudinal and relaxation of the circular fibres of the rectum. Stimulation of the hypogastrics causes the reverse effects. Commenting upon this theory and Fellner's later experiments, Langley and Anderson write:[2] "We do not wish to assert that this theory applies in no case, but most certainly it is not one of general application. According to this theory the descending colon of the rabbit should receive from the lumbar nerves no inhibitory fibres for its longitudinal coat, and from the sacral nerves no motor fibres for its circular coat. In fact, when due care is taken inhibition of the longitudinal coat is produced by the lumbar nerves with undeniable distinctness; and the contraction of the circular coat produced by the sacral nerves is, at its best, one of the most striking visceral actions that can be brought about by stimulating any nerve in the body. At the same time we must state that our

[1] *Pflüger's Archiv*, vol. lvi., p. 542, 1893.
[2] *Journ. of Phys.*, vol. xviii., p. 104, 1895.

experiments do not disprove the statements of Fellner with regard to the innervation of the rectum in the dog, they only suggest that further observations are desirable."

We should note, however, that Gaskell[1] "entirely endorses" Fellner's conclusion. He obtained in the dog contraction of the longitudinal fibres of the rectum on stimulation of the nervus erigens, while, when the hypogastrics were stimulated, a distinct peristaltic contraction was observed. In the frog, too, he showed that fibres occurred in the seventh nerve, which, when stimulated, caused contraction of the circular muscles, and that the eighth and ninth nerves contained fibres stimulation of which caused contraction of the longitudinal muscles and pulling down of the rectum.

Langley[2] describes the effect of stimulation of the fibres of the upper region as inhibition of the descending colon and rectum, sometimes preceded by a brief contraction. The inhibition affects both longitudinal and circular fibres. The set of fibres from the sacral region produce a strong contraction of both sets of muscle.

With regard to the spinal roots, through which these two sets of fibres leave the cord, Bechterew and Mislawski[3] describe them as being the upper lumbar roots down to the sixth or seventh, and also the third sacral. The whole question has lately been closely gone into by Langley and Anderson.[4] In the rabbit the roots are the second to fifth lumbar inclusive, the third and fourth sacral, and, as a rule, either the second sacral or the first coccygeal. In the cat the second to fourth lumbar, the second and third sacral, and either the fifth lumbar or the first sacral. In the dog the origin of the lumbar fibres is slightly more anterior, and that of the sacral slightly more posterior than in the cat. The upper set of fibres in the rabbit causes, when stimulated, inhibition of the intestinal muscles (circular and longitudinal), sometimes a preliminary contraction which

[1] *Journ. of Phys.*, vol. vii., p. 26, 1885.
[2] *Ibid.*, vol. xii.; *Proc. Physiol. Soc.*, p. 23, 1890.
[3] *Arch. f.* (*Anat. u.*) *Phys.*, suppl., p. 243, 1889.
[4] *Journ. of Phys.*, vol. xviii., p. 67, 1895.

is then usually a circular contraction, only occasionally a longitudinal contraction. In the cat the same results are obtained, but are less marked because the intestines are more quiescent when exposed. The lower set causes contraction of both circular and longitudinal coats of rectum and descending colon and of the recto-coccygeal muscle. In the cat the same results were obtained, though contraction of the circular coat was not so constant, and when obtained was slight and took place slowly. With regard to their course, Langley and Anderson have shown by the degeneration method[1] and by the nicotine method[2] that the upper set of fibres run from the lumbar nerves to the inferior mesenteric ganglia direct, and there nearly all end in cells of that ganglion. Hence they run by branches from these ganglia—as colonic nerves—directly to the viscus. In the case of the second set of nerves, ganglion cells are present, and are placed near the viscus itself. Thus the upper set of nerve fibres are homologous with the related fibres contained in the splanchnics, the lower set with those in the vagi. With regard to the part played by the plexuses of Meissner and Auerbach, they were not able to obtain any special evidence of function. They conclude that the cells of these plexuses do not belong to the sympathetic system, but are of a different class.

Vaso-motor fibres for this part of the alimentary canal are found in both the upper and lower set of fibres. Stimulation of the upper set causes marked pallor of the descending colon and rectum, and of the mucous membrane of the anus. There are no vaso-dilators in this set. The cells on the course of the fibres are in the inferior mesenteric ganglion, or in the colonic nerves near their origin from that ganglion. The sacral set of fibres contain vaso-dilator fibres for the rectum, but they were not observed for the colon. The effect was not very marked in the cat, but rather better in the rabbit. These fibres have cells on their course placed near their termination in the viscus.

Steinach, for the frog finds nerves to the rectum in both

[1] *Journ. of Phys.*, vol. xvii., p. 177, 1894.
[2] *Ibid.*, vol. xix., p. 131, 1895.

anterior and posterior roots of the sixth and seventh spinal nerves. He obtains reflex contractions from stimulation of the posterior roots of one side after section of all the anterior roots on both sides, and of the posterior on the side stimulated.

The anus.—Sherrington,[1] when making observations on the fibres of the anterior roots forming the lumbo-sacral plexus, describes that when all the anterior roots of this region were cut the anus remained closed but less retracted than usual. On being opened by a sound it remained open after the sound was removed, but that on stimulation of some of these roots the anus being open, it was smartly closed by a contraction of the sphincter muscle. The roots which were effective in the cat were the eighth and ninth post-thoracic, sometimes the seventh. In Macacus, the root was the eighth, and either the seventh or ninth, though always to a less extent. When one root remained intact it did not remain patulous, and no asymmetry was produced by section of all three roots on one side. On excitation of a root when the anus was patulous a symmetical contraction was obtained if the stimulus was strong, if weak sometimes an asymmetrical contraction was produced. Langley and Anderson[2] describe the upper set of fibres to contain in a rabbit inhibitory fibres for the internal sphincter, and obtained some evidence which, however, they did not consider very satisfactory, of motor fibres. In addition these fibres contained motor fibres for the non-striated muscles beneath the skin in the neighbourhood of the anus. These fibres chiefly innervated the half of the corresponding side. The origin from the cord was rather more restricted than for those fibres which innervated the colon and rectum. In the cat this set, on stimulation caused marked contraction of the internal sphincter. Stimulation of the sacral set of fibres in the rabbit caused dilatation of the internal sphincter ani which was usually followed one or two seconds after cessation of the stimulus by a marked contraction. There are thus motor fibres for this muscle

[1] *Journ. of Phys.*, vol. xiii., p. 672, 1892.
[2] *Loc. cit.*

in these nerve roots. In the cat stimulation of these fibres may result in contraction or dilatation of the sphincter. The nerve cells on the course of the fibres of the upper set lie either in the superior mesenteric ganglia or in the ganglia in the hypogastric nerves. The cells on the lower set lie near the peripheral termination of the fibres.

Spleen.—Until the present year our knowledge of the innervation of this organ rested chiefly upon the work of Bulgak and Roy. Bulgak[1] relied upon direct observation of the spleen and showed that the nerves in the gastro-splenic omentum were of two kinds, afferent and efferent. Stimulation of the peripheral end of the latter caused a marked contraction of the spleen which was observed to pale in colour, its edges became more rounded and irregularities on its surface appeared. Stimulation of the peripheral end of the former nerves caused no effect, but when the central end was stimulated a marked reflex contraction was produced. He obtained big contractions by stimulating the semilunar ganglion or the peripheral end of the greater splanchnic on the left side. He observed no contraction on stimulating the peripheral end of the lesser splanchnic on the left side, or of either splanchnic on the right side. He traced these fibres still further backwards in their course, and localised them to the third to tenth thoracic anterior roots of the left side only, stating that no contraction was to be obtained by stimulating any of the roots above or below these or on the opposite side. He next examined the effect of the vagus upon the spleen and in opposition to previous observers found that stimulation of the nerve did not produce any contraction. The nerve was stimulated both above and below the point where it gave off its cardiac branches. Stimulation of the central end produces a large contraction, an effect which he suggests, is due to the interference with respiration, for he had previously observed that the splenic contractions were greatly increased by a venous condition of the blood. Roy[2] studied the rhythm and innervation of this organ by

[1] *Virchow Archiv*, lxix., p. 181, 1877.

[2] *Journ. of Physiol.*, vol. iii., p. 203, 1881.

employing his special plethysmographic method. He showed that the rhythmic contractions of the spleen might vary largely under different conditions. He obtained powerful contractions of the organ on stimulation of either splanchnic nerve and further differed from Bulgak in obtaining marked splenic contractions on stimulating the peripheral end of the cut vagus.

Quite recently a paper has appeared by Schäfer and Moore [1] in which this question is fully discussed. They show that the rhythm of the splenic contractions is quite independent of the nerves running to it though modified by them. Stimulation of either splanchnic in both dogs and cats produces a powerful contraction, better by the left nerve than by the right. In one case weak stimulation of the left splanchnic produced a dilation, whilst stronger and more frequent stimulation of the same nerves produced the ordinary contraction. In determining the outflow from the spinal cord they showed that the fibres in the splanchnic running to the spleen leave the cord in the anterior roots of both sides from the third to fourteenth post-cervical nerves inclusive. They are present in largest numbers in the sixth, seventh and eighth, and in fair numbers in the fifth, ninth and tenth. Of the similar roots of the opposite sides those on the left side produce a more marked effect than those on the right. In one case in a cat the same result was obtained. These results are all the more decisive in that they are able to obtain very sensitive records by employing a specially devised plethysmograph that is much simpler and more sensitive than Roy's instrument. They further investigated by the employment of the nicotine method as to whether there were any cells on the course of these fibres. Doses of five milligrammes, in succession, were administered by injection, and between each dose the nerves were tested in three parts of their course, in the anterior root, in the splanchnic, and at the hilum of the spleen. They thus show that there is a cell station which is easily paralysed by nicotine in the ganglia of the

[1] *Journ. of Physiol.*, vol. xx., p. 1, 1896.

sympathetic chain, and, moreover, that there is possibly a second series of cells, less readily paralysed by nicotine, between the splanchnics and the spleen, probably that is, in the semilunar ganglia. In connection with the position of the cells on these fibres, it should be noticed that these experimenters localise them to the lateral chain of ganglia, but that in the case of the nerves to the muscles of other viscera, intestines, etc., they have always been found to lie in the collateral ganglia. In regard, moreover, to the position of the cells on the vaso-motor fibres to the spleen, Schäfer and Moore's experiments point to a similar position for the majority of them. This view has been strongly questioned by Langley[1] who believes that, with the exception of a few aberrant fibres, all the vasco-constrictors of the splanchnics are in connection with cells of the solar plexus and of this plexus only.

NERVES TO THE GLANDULAR STRUCTURES OF THE RESPIRATORY AND ALIMENTARY TRACTS.

The trachea and larynx.—An increase in the rate of secretion of mucus from the glands in the mucous membrane of the trachea as a result of nerve stimulation has recently been proved by Kokin.[2] He experimented upon dogs and cats in which the trachea was laid open longitudinally in the mid-line by a galvano-cautery. The surface was then carefully dried and adherent mucus removed, and the time interval which elapsed before small, rounded drops of mucus appeared at the mouths of the ducts was noted. The same was repeated while various nerves were stimulated. Kokin thus finds secretory fibres in the vagus for these glands. In the dog the secretory fibres for the larynx and upper and middle portions of the trachea run in the superior laryngeal branch of the vagus. In the cat the inferior laryngeal contains fibres for the trachea and lower half of the larynx.

To the submaxillary gland.—In the cat Langley[3] has

[1] *Journ. of Physiol.*, vol. xx., p. 223, 1896.
[2] *Pflüger's Archiv*, vol., lxiii., p. 622, 1896.
[3] *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.

shown that the secretory fibres to the submaxillary gland leave the cord mainly in the second and third thoracic nerve roots; once only has he obtained secretion from the first, fourth or fifth thoracic. In the dog the origin is slightly different. In this animal the first and second thoracic always contain secretory fibres, the third, fourth and fifth only containing some in one out of three cases.

These fibres end in cells of the superior cervical ganglion.[1] Thence passing through the grey rami of the ganglion the fibres reach the gland *via* the sympathetics on the carotid and facial arteries. There are no further cells on these fibres. The position of the cells on the course of these sympathetic secretory fibres has also been located to the superior cervical ganglion by the aid of the method of degeneration. This has been effected by Langley[2] and by Bradford[3] for the cat.

The chorda tympani fibres to the gland have also been shown to possess nerve cells on their course. In the dog these[4] are found on the course of the chorda tympani just at its entrance into the hilum of the submaxillary gland or shortly before this. In the cat many more are found in the nerve before its entrance into the gland. The præganglionic fibres therefore are from the origin of the seventh cranial nerve along the chorda to its termination at the gland; and the post-ganglionic from this point to their distribution in the gland substance. Langley also shows that the cells in the submaxillary ganglion and in the triangle lying between the duct, the lingual nerve and the chorda, are in connection with fibres to the sublingual gland not to the submaxillary.

By the injection of nicotine the sympathetic cells are paralysed before the chorda cells, in the cat, and recover later. In the dog they however recover quickly.

The *vaso-constrictor* fibres to the submaxillary gland

[1] Langley and Dickinson, *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889, and Langley, *Journ. Physiol.*, vol. xi., p. 123, 1890.

[2] *Journ. of Physiol.*, vol. vi., p. 87, 1885.

[3] *Ibid.*, vol. ix., p. 302, 1888.

[4] *Loc. cit.*

arise from the thoracic cord in the same roots as the secretory fibres and run up the cervical sympathetic to the superior cervical ganglion where they terminate. From the nerve cells influenced by them the post-ganglionic fibres run along the carotid and facial nerve-plexuses and so reach the gland. There are no other nerve cells on the course of the fibres running up the cervical sympathetic other than those in the superior cervical ganglion.[1]

With regard to the *vaso-dilators* to the submaxillary and sublingual glands passing along the chorda-tympani, Langley[2] has shown that those for the submaxillary gland are in connection with cells in the chorda-tympani at or near its entrance into the hilum of the gland; those for the sublingual gland have their cells in the submaxillary ganglion, or in the triangle formed by the duct, the lingual nerve and the chorda tympani.

For an account of what is known of the secretory fibres to the stomach and pancreas, I would refer to the recent number of "SCIENCE PROGRESS"[3] containing Starling's paper, "Pawlow's Researches on the Physiology of Secretion".

To the liver.—Bernard observed that an increase in the amount of glucose in the blood, and a consequent glycosuria could be brought about by stimulation of the central end of the divided vagus, or better by alternate stimulation of the central and peripheral ends. He further noted that on the death of an animal consequent on section of both vagi in the neck there was a complete disappearance of sugar from the blood and from the tissues generally.

E. Cavazzani[4] found changes in the liver cells following stimulation of the cœliac plexus in dogs and rabbits which were comparable to changes occurring in glands on stimulation of their nerves. On comparing the appearances of the cells in a piece of the liver which had been stimulated

[1] See Langley, *Journ. of Physiol.*, vol. xi., p. 153, 1890, and Langley, *Journ. of Physiol.*, vol. vi., p. 87, 1885.

[2] *Journ. of Physiol.*, vol. xi., p. 123, 1890.

[3] Feb., 1896, vol. iv., p. 491.

[4] *Pflüger's Arch.*, vol. lvii., p. 81.

in this way, with cells from a second portion of the same liver which had been at rest, he observed histological differences exactly comparable to the appearances of liver cells taken from fasting and from well-fed animals.

Butte [1] repeated Bernard's experiments on section of the two vagi in the neck. The dogs died from twenty to forty-six hours after the section, and in no case was any glycogen found in the liver. In other experiments he [2] also showed, in confirmation of Bernard's original observation, that stimulation of the peripheral end of the divided vagus causes a diminution of the amount of glycogen in the liver, and an increase in the amount of glucose in the blood.

Cavazzani[3] shows that this same result may be obtained by stimulation of the cœliac plexus in dogs, and that the quantity of glycogen disappearing corresponds to the quantity of glucose formed.

Levene[4] confirms this production of glucose on vagus stimulation, but still found glycogen in the liver, and sugar in the blood, three days after section of both vagi.

Morat and Dufourt [5] show that the sugar formation is due to nervous action not to alterations in the circulation of the liver. In a later paper [6] they show that stimulation of the splanchnics, by induction shocks after division, or by asphyxia, leads to a disappearance of glycogen and a corresponding increase in the amount of glucose. This is obtained both while the circulation is intact or when it is stopped by ligature of the aorta and portal vein.

Vascular nerves to the liver.—By simultaneous records of the aortic blood pressure, and that in the portal vein, Bayliss and Starling [7] have mapped out the spinal origin of the constrictor fibres to the portal vein. These leave the cord in the third to eleventh thoracic roots inclusive, only

[1] *Comp. Rend. Soc. de Biol.*, vol. xlvi., p. 734, 1894.

[2] *Ibid.*, p. 166, 1894.

[3] *Ann. di chimica e farmacologia*, Bologna, 1894, abstracted in Maly's *Jahres-Bericht*, vol. xxiv., p. 391, 1895.

[4] *Centr. f. Physiol.*, vol. viii., p. 337, 1894.

[5] *Compt. Rend.*, vol. cxviii., p. 659.

[6] *Arch. de Physiol.*, vol. xxvi., p. 371, 1894.

[7] *Journ. of Physiol.*, vol. xvii., p. 120, 1894.

a few being found in the third and fourth, and tenth and eleventh anterior thoracic roots. The nerves to the hepatic artery have been investigated by Cavazzani and Manca.[1] Their method was to establish an artificial circulation and then determine the amount of outflow under different circumstances. They find vaso-dilators in both the splanchnic and vagus, and constrictors in the splanchnic. Asphyxia causes a dilation which is not produced when the vagi are cut. Stimulation of the cœliac plexus low down causes better dilatation than stimulation of the vagus.

Innervation of the Thoracic duct.—By determinations of the rate of outflow of a fluid at constant pressure passing through the Thoracic duct, Camus and Gley[2] have obtained evidence of the presence of nerves, causing both dilation and constriction of the duct, in the sympathetic chain under the first thoracic ganglion. As a rule the dilator effect is produced.

NERVES TO THE GENITO-URINARY SYSTEM.

To the kidney.—Bradford[3] has determined the origin of the vascular nerves to the kidney by observations of the changes in its volume on excitation of the various anterior roots. He finds that the vaso-constrictors are mainly contained in the eleventh, twelfth, and thirteenth thoracic nerves, to a less extent in the seventh, eighth, ninth, and tenth thoracic, and sometimes in the sixth thoracic and first and second lumbar nerves. He determined the presence of vaso-dilator nerves by stimulating with induced shocks, repeated only once per second, or once in two seconds. By this method he was able to show the existence of dilator fibres to the kidney in the eleventh, twelfth, and thirteenth thoracic nerves.

Langley and Dickinson[4] have shown that the nerve cells on the course of the constrictor fibres are situated in the cœliac, mesenteric, or renal ganglia, and that the cells

[1] *Arch. Ital. de Biol.*, vol. xxiv., pp. 33 and 295, 1895.
[2] *Arch. de Physiol.*, vol. vii., pp. 301, 328, 1895.
[3] *Journ. Physiol.*, vol. x., p. 358, 1889.
[4] *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889.

on the course of the dilator fibres are placed in the solar plexus and renal ganglia.

The bladder.—When considering the innervation of this viscus we have again to note that we are dealing with one which, as commonly described, possesses a double muscular wall and a double nerve supply, an upper one from the lumbar nerves and a lower from the sacral *viâ* the nervi erigentes. With regard to the question of the reversed function of the two sets of fibres on the two muscular coats (v. Basch's theory), we have evidence leading to a similar conclusion as in the case of the colon. Thus Griffiths[1] brings evidence of an anatomical nature that in reality we have to deal with a viscus possessing a single muscular wall. Zeissl,[2] on the contrary, argues from his experiments that the sacral set cause, when stimulated, contraction of the detrusor urinæ and inhibition of the sphincter, and that the hypogastrics cause contraction of the sphincter and inhibition of the detrusor urinæ, though the evidence of this last action he does not consider very satisfactory. Langley and Anderson, however, take the opposite view, and consider that the interpretation which Zeissl has placed upon his results is not the correct one. Their experiments show that stimulation, of both the hypogastric and pelvic (nervus erigens) nerves, causes contraction of both longitudinally and circularly arranged muscle bundles.

In reviewing the experiments of those who have been working in recent years upon the origin and course of fibres which innervate the bladder, we may first notice those of Navrocki and Skabitschewski,[3] who worked upon curarised dogs, and observed the movements of the bladder directly by the naked eye. This method they chose as the only one giving certainly reliable results, for they found that the introduction of a catheter, or tying in a tube into the apex of the bladder, led to irregular contractions, which tended to make results by such methods unreliable. The

[1] *Journ. of Anat. and Phys.*, vol. xxv., p. 535, 1891.
[2] *Pflüger's Archiv*, vol. liii., p. 560, 1893.
[3] *Ibid.*, vol. xlviii., p. 335, 1891.

upper set of fibres they traced passing through the fourth and fifth anterior lumbar roots, to the sympathetic chain by white rami communicantes, thence by the mesenteric nerves to the inferior mesenteric ganglion, then along the hypogastrics to the hypogastric plexus, and so by the vesical plexus to the bladder. The lower set left the cord in the second and third sacral nerves, and reached the hypogastric plexus by the pelvic nerve, and so on to the bladder. Stimulation of either of these two sets caused marked contraction of the bladder.

Sherrington[1] recorded the movements of the bladder, consequent upon stimulation of the anterior roots of the lumbar and sacral nerves, by means of a water manometer connected to the interior of the bladder by a catheter. In the cat he describes the effective roots, as being the third and four lumbar, together with either the second or fifth, or occasionally both. Of the lower set the second sacral was the chief root, and the first and third usually contained fibres having this function. In Macacus Rhesus he found the third and fourth lumbar with either the second or fifth, and the second sacral with the first and third to less extent. The lower set always produced the more powerful contraction which was unilateral when a nerve root of one side was stimulated.

Griffiths[2] found that stimulation of the pelvic nerve produced a more powerful contraction than stimulation of the hypogastric, but that both of them produced contraction throughout the entire thickness of the muscular coat. Stimulation of the nerves on one side produced unilateral contraction of the bladder. Langley and Anderson[3] found that stimulation of either set of nerves caused contraction of the whole muscular coat, but did not get a unilateral contraction on stimulating the nerves of one side, though the contraction on the same side was much better marked than on the opposite side. The upper set of fibres left the cord in either the second and third or third and fourth, or fourth

[1] *Journ. of Phys.*, vol. xiii., p. 677, 1892.
[2] *Journ. of Anat. and Phys.*, vol. xxix., pp. 61 and 254, 1895.
[3] *Journ. of Phys.*, vol. xix., p. 71, 1895.

lumbar roots in the dog; in the cat chiefly by the fourth occasionally by the third and fifth, and in the rabbit by the fourth and fifth, together with either the third or second lumbar.

These fibres pass, by the mesenteric nerves, from the sympathetic chain to the inferior mesenteric ganglion, thence by the hypogastrics to the bladder. Nerve cells in their course can be shown by the nicotine method. They are either situated in the inferior mesenteric ganglion or along the course of the hypogastrics. Stimulation of this set causes a much weaker contraction than stimulation of the sacral set, a contraction not sufficiently powerful to cause micturition. The lower set of fibres occur, in the rabbit, in the third and fourth sacral with a few in the second, or in the second and third sacral with a few in the fourth; in the cat, in the second and third sacral, occasionally in the first, and in the dog, in the second and third sacral with sometimes a few in the first coccygeal. Stimulation of these fibres causes micturition. They reach the bladder *via* the pelvic nerves and hypogastric plexus. Their course is broken by nerve cells which occur scattered along the course of the fibres usually near the viscus itself, *e.g.*, in its lateral ligament. Inhibitory fibres were looked for but without any positive result; they consider that if any be present they are only few in number. Recently Courtade and Guyon[1] have published results of experiments upon this subject which, however, only confirm some of our previous knowledge. They are apparently unacquainted with the papers of Sherrington, Griffiths, and Langley and Anderson.

In the frog Gaskell[2] found two sets of fibres corresponding to those in mammals. The lower set occur in the eighth and ninth spinal nerve roots, and stimulation of them caused marked contraction of the longitudinal coat. The upper set are represented by fibres in the seventh nerve, which he describes as causing contraction of the

[1] *Arch. de Phys.*, vol. xxviii., p. 622, 1896.
[2] *Journ of Phys.*, vol. vii., p. 26, 1886.

circular fibres. Bernheim[1] in frogs and salamanders found fibres for the bladder in the eighth and ninth nerves, sometimes in the tenth as well. Steinach[2] found nerves for the bladder of the frog not only in the anterior roots of the seventh, eighth and ninth nerves, but also in the posterior roots of those same nerves. He confirms their presence in these posterior roots, by obtaining a reflex contraction of the bladder after all the anterior roots of these nerves had been cut on both sides, and the posterior as well on one side.

Very few, if any, *vaso-motor* nerves are contained in the lumbar set of nerves[3] to the bladder, nor were Langley and Anderson able to show their presence in the sacral set of fibres.[4]

External genital organs.—Langley and Anderson[5] have examined the lumbar and sacral nerves with especial reference to these organs.

Here again the nerves arise in two sets, an upper and a lower. The upper set of nerves in the male cause when stimulated a powerful contraction of the retractor muscle of the penis, contraction of the intrinsic muscles of the penis, of the unstriated muscles of the genital skin, and of the dartos and cremaster muscles. Stimulation of the lower set of fibres causes very marked inhibition of the retractor muscle, of the non-striated muscles of the penis and of the skin, with contraction of the striated erector muscles, *viz.*, the recto-cavernosus, the ischio cavernosus, the bulbo-cavernosus, Houston's muscle and the striated muscle of the urethra. In the female, the upper set cause contraction of the vulva and of the skin muscles, with slight retraction of the clitoris; the effects sometimes are very slight especially in the cat and dog. The lower set cause dilatation of the vulva, relaxation of the skin muscles around the vulva and contraction of the muscles which correspond to the

[1] *Arch. f.* (*Anat. u.*) *Phys.*, suppl., p. 11, 1892.
[2] *Pflüger's Archiv*, vol. lx., p. 593, 1895.
[3] *Journ. of Phys.*, vol. xix., p. 75, 1895.
[4] *Loc. cit.*, p. 79.
[5] *Journ. of Physiol.*, vol. xix., p. 85, 1895.

striated genital muscles of the male. The upper set of fibres leave the cord in the cat either in the third and fourth lumbar with a few in the fifth, or in the fourth and fifth with a few in the third, occasionally there are some in the second. In the dog their origin is a little more anterior, for there are never any in the fifth. In the rabbit they pass out in the third, fourth and fifth. Sherrington [1] observed contraction of the cremaster muscle on stimulation of the second and third anterior roots of lumbar nerves in rhesus, in one case the fourth lumbar was found to be effective instead of the second.

The posterior set, in the cat, are found in the first and second, occasionally in the third sacral; in the rabbit in the second, third and fourth sacral anterior roots. Sherrington [2] observed a sharp closure of the vaginal orifice on stimulation of the second and third sacral nerves in the cat, and in rhesus. As a rule the third nerve was more effective than the second, and the contraction was bilateral.

The course of the upper set of fibres is by the white rami to the sympathetic chain, whence they may travel by two paths, either to the pudic nerve or *viâ* the pelvic plexus. The great majority of the fibres leave the chain by the sacral grey rami to the sacral nerves, and reach their destination by the dorsal nerves of the penis or clitoris, the genito-anal and the scrotal nerves. A certain number of this set—but relatively few—run by the hypogastric nerves. The viscero-inhibitory fibres in the sacral nerves all pass into the pelvic visceral branches of those nerves. The fibres to the striated erector muscles run direct through the perineal nerve, genito-anal nerves and the nervus dorsalis.

The upper set of fibres have nerve cells upon them which for those which travel by the sacral grey rami are placed in the sacral ganglia, for those which travel by the hypogastric are placed in the hypogastrics or a little nearer their peripheral ends.

Of the lower set of fibres those which run to striated muscles resemble ordinary motor nerves, and have no nerve

[1] *Journ. of Physiol.*, vol. xiii., p. 683, 1892.
[2] *Ibid.*, p. 675, 1892.

cells on their course. The inhibitory fibres passing through the nervi erigentes have cells on their course, placed close to the urethra or in the organs themselves.

Vaso-motor nerves to these parts.—Stimulation of the lumbar set of fibres causes strong contraction of the arteries to the penis or clitoris, and a slighter contraction of the vessels to the surrounding genital skin and scrotum. The origin of these fibres from the cord is in the main similar to that given above, though in the cat the thirteenth thoracic and first lumbar were also effective.

The nerve cells on the course of these fibres are placed similarly to those on the other visceral fibres running from the lumbar set. They did not find any satisfactory evidence of the presence of vaso-dilators in these fibres. The lower set of fibres contain many vaso-dilators but no vaso-constrictors. Gaskell[1] found vaso-dilators to the penis in the second and third sacral anterior roots in the rabbit. They were never present in any posterior roots. Sherrington[2] obtained the same result in rhesus and in the cat. Francois Franck[3] investigated the vascular nerves to the penis by a plethysmographic method, and recorded at the same time the changes in arterial and venous pressure in the organ. He finds that the mesenteric nerves to the inferior mesenteric ganglia from the sympathetic chain contain many vaso-dilators, and also vaso-constrictors though in fewer numbers. The pelvic nerves contain many vaso-dilators. His experiments were carried out upon dogs which were curarised in order to prevent complications by other muscular influences.

Internal generative organs.—Our knowledge of the innervation and course of the fibres to the internal generative organs also largely depends upon the researches of Langley and Anderson.[4] They find that for these pelvic viscera there is only one set of nerves, which come from the lumbar roots. These cause very strong contraction of the

[1] *Journ. of Physiol.*, vol. viii., 1887. *Proc P. S.*, p. 4.
[2] *Ibid.*, vol. xiii., p. 686, 1892.
[3] *Arch. de Physiol.*, vol. xxvii., pp. 122 and 138, 1895.
[4] *Journ. of Phys.*, vol. xix., p. 122, 1895.

muscular coat of the uterus and vagina, or of the vas deferens and vesiculæ seminalis (uterus masculinus) in the rabbit. In the cat the same contraction results though not to so marked an extent. The contraction involves both muscular coats. In the dog the contraction of the vas is not well marked, the longitudinal contraction which is so marked a feature in the rabbit is almost absent; this is to be associated with the fact that in the dog the longitudinal muscular coat is poorly developed. Unilateral stimulation of the nerves causes unilateral contraction of the vas, but bilateral contraction of the vesicula seminalis—a contraction which is strong enough to eject semen. These fibres occur chiefly, in the rabbit, in the fourth lumbar and to a less extent in the third and fifth anterior lumbar roots. In the cat they are found chiefly in the third and fourth with a few in the second lumbar.

Sherrington[1] observed contraction of the vas to occur as the result of stimulation of the second and third lumbar anterior roots in rhesus; in the cat from the third and fourth lumbar. The contraction had a long latent period and was of a peristaltic nature, involving both muscular coats. In the female contraction of the fibres in the round ligament followed stimulation of the second and third lumbar, or sometimes in the fourth lumbar in rhesus, and of the third and fourth lumbar in the cat.[2] In rhesus this muscle is striated. Langley and Anderson also note contraction of the unstriated fibres in the meso-metrium on stimulating the lumbar nerves.

The fibres leave the corresponding nerves as white rami and pass to the sympathetic chain, whence, as a rule, they pass to the inferior mesenteric ganglion, and by the hypogastric nerves to the pelvic plexus and their final distribution. The nerve cells on the course of these fibres are situated either in the inferior mesenteric ganglion or in ganglion cells placed further on their course in the hypogastric nerves. This has been proved by the nicotine method, and also by examination of the fibres after de-

[1] *Journ. of Phys.*, vol. xiii., p. 685, 1892.
[2] *Loc. cit.*, p. 684.

generation of the preganglionic segment has been brought about by section of the lumbar nerves.[1]

With regard to the question of the presence of a second set of fibres in the sacral nerves, Langley and Anderson are not able to confirm the observations of previous workers that such exist. They obtained negative results on stimulating the sacral nerves, and were, moreover, led to the same conclusion, as a result of the tracing of degenerated fibres following section of the sacral nerves.[2]

The *vaso-motor* nerves to these parts take the same course as the fibres to the muscular walls. Stimulation of the efficient nerves causes, in addition to the previously mentioned effects, marked pallor of uterus, vagina, and vestibule in the female, and of the vas and seminal vesicles in the male. They have the same course and similar nerve-stations as the viscero-motor fibres.

NERVES TO SWEAT GLANDS.

Langley,[3] working upon the sweat glands in the pads of the cat's feet, describes the origin of the fibres for the fore feet to lie in the fourth to tenth thoracic inclusive. They mainly run in the sixth, seventh, and eighth thoracic anterior roots, to a less extent in the fifth and ninth, still less in the fourth, and only occasionally in the tenth thoracic. All these fibres run upwards, and end in cells in the ganglion stellatum. From this they issue in the grey rami to the nerves of the brachial plexus, and thence to their distribution. The combined sixth and seventh white rami supply chiefly the inner part of the foot.

For the hind foot they leave the cord in the first and second lumbar, to a rather less extent in the thirteenth thoracic, and still fewer in the twelfth thoracic and third lumbar; and when the lumbo-sacral plexus is posterior in the fourth lumbar. None of these fibres leave the sympathetic cord above the sixth lumbar ganglion or below

[1] *Journ. of Phys.*, vol. xviii., p. 177, 1894; vol. xix., p. 372, 1896.

[2] *Ibid.*, vol. xix., p. 372, 1896.

[3] *Ibid.*, vol. xii., p. 347, 1891; vol. xvii., p. 296, 1894-5. A full account of the earlier literature is given in this paper.

the second sacral. They pass out from the sixth and seventh lumbar and first and second sacral ganglia, being connected with cells in those ganglia. As a rule the fibres leaving in a grey ramus of a ganglion are connected to the cells in that ganglion, but in a few cases the cells are situated in the ganglion above. In a few cases none are found in the second sacral, and then nearly always the lumbo-sacral plexus is found to be of the anterior type. Those fibres given by the sixth ganglion are chiefly supplied to the inside of the foot, and those from the second sacral to the outside. Stimulation of the grey ramus from the first sacral causes a marked secretion on the outer side, and a less prominent secretion on the inner side. Stimulation of the seventh lumbar gives a less regular result, commonly there is a secretion all over the foot, sometimes more marked on the inner side.

There are no secretory fibres running directly to the glands from the cord through the sciatic roots.

NERVES TO THE EYEBALL.

As recorded by Bernard,[1] it was Biffè who first showed that stimulation of the upper end of the cut cervical sympathetic caused dilation of the pupil. Petit,[2] from a study of the course of the fibres from the fifth and sixth thoracic nerves into the cervical sympathetic, as given by Willis and Vieussens, came to the conclusion, in opposition to them, that the fibres were running from the cord to the neck, not in the reverse direction. To test this, he cut the cervical sympathetic, and discovered that the pupil was permanently constricted.

Budge and Waller[3] also found that stimulation of the peripheral end of the cut cervical sympathetic caused dilation of the pupil, an effect not to be obtained on stimulation of the nerve one month after its section. By stimulation of the spinal cord, they obtained this dilatation

[1] *Journ. de Physiol.* (Brown-Séquard), vol. v., p. 383, 1862.
[2] *Histoire de l'Académie des Sciences*, 1727.
[3] *Comp. Rend.*, vol. xxxiii., pp. 370, 418, 1851.

effect best, on stimulating at the second and third thoracic segments, and came to the conclusion that these two nerves are those carrying the fibres. They further traced the fibres as passing through the Gasserian ganglion into the ophthalmic branch of the fifth cranial nerve. Bernard[1] observed in addition a drawing back of the eyeball and a fall of the eyelids after section of the nerve. By cutting both the first and second thoracic anterior roots he obtained the same result. Langley and Dickinson[2] showed, by the nicotine method, that there were nerve cells on the course of these fibres, which are situated in the superior cervical ganglion. By stimulation of the anterior roots, Langley[3] finds that in the dog and cat the fibres leave by the first and second thoracic nerves, occasionally by the third, though as a rule these latter only run to the nicitating membrane and eyelids. In the rabbit the second and third thoracic are the chief nerves, the first exerting but slight action. There are no other nerve cells on their course other than those in the superior cervical ganglion.

Nerves to the splincter iridis and ciliary muscle.—Langley and Anderson[4] have shown that at any rate the main number of cells in the ciliary ganglion, are on the course of the fibres to these muscles. After the injection of ten milligrams of nicotine, stimulation of the third nerve produces no effect, though stimulation of the short ciliary nerves still produces the usual result.

On a review of the whole of the facts of the general efferent innervation of the structures developed from the splanchnic mesoblast, we find that we may draw certain generalisations.

In all thoroughly investigated cases, the nerve chain uniting the central nervous system with the peripheral organ consists of two links, each consisting of a nerve cell and its fibre. The upper one, with its cell placed

[1] *Comp. Rend., Soc. de Biol.*, vol. iv., pp. 155, 168, 1852; and *Comp. Rend*, vol. xxxvi., p. 375.

[2] *Proc. Roy. Soc.*, vol. xlvii., p. 379, 1889-90.

[3] *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.

[4] *Journ. of Physiol.*, vol. xiii., p. 460, 1892.

in the central grey matter, terminates dendritically at the position of the second nerve cell. The second cell is found situated in various positions, either in the lateral chain of ganglia, *i.e.*, those having a white ramus running to them, or in the collateral ganglia such as the superior cervical ganglion, or the mesenteric ganglia, or finally, in peripheral ganglia placed in or very near the organs themselves, *e.g.*, in the heart, the internal generative organs, etc. In his latest paper, Langley[1] gives, as the conclusion he has drawn from his many experiments, that "each visceral nerve fibre has one nerve cell on its course and one only. More accurately, that a visceral nerve impulse on its way from the central nervous system to the periphery traverses one nerve cell and one only." He considers that each fibre which leaves the central nervous system divides, and that each division is connected with a nerve cell. As a rule all the divisions terminate in the same ganglion, but in some cases there is evidence to show that one or more of the collateral divisions may terminate in a second ganglion, or along a nerve strand, proximally or distally to the termination of the major number of the divisions. Further, that where there are several præ-ganglionic fibres running to the same or to analogous parts, they nearly all terminate in the same ganglion, though here again exceptions may occur, some few fibres terminating with a slightly shorter or longer course.

In many cases the post-ganglionic fibre is non-medullated, but this is by no means a general rule, for Langley[2] has shown that many finely medullated fibres occur in grey rami and elsewhere which are neurons from cells in the various ganglia.

A point of considerable interest is with regard to the part played by the nerve cell which is interpolated upon the course of the fibres uniting the viscera to the centre. Reflexes may be obtained from some of these ganglia, but Langley and Anderson have shown that these reflexes are

[1] *Journ. of Physiol.*, vol. xx., p. 223, 1896.
[2] *Ibid.*, p. 55, 1896.

not true reflexes, as they occur in the grey matter of the cord, but are probably due to the stimulus running up an efferent fibre and down a collateral of that same fibre and so bringing about the muscular contraction. Another view of the part played by the cells is that through them the fibre loses its medulla and becomes non-medullated; but this we have seen is not general. There is a final suggestion that a few nerve fibres run to these cells, and that many more fibres run from them. That, in a way then, there is a multiplication of fibres as they travel through the ganglion, a point which will require only a few fibres to run from the cord and yet readily allow of a wide peripheral distribution. This is of course an obvious advantage where a large peripheral area is always required to work as a whole and in the same sense.

The general arrangement of the nerve cells anatomically as contrasted physiologically also shows some uniformity, and allows us to draw conclusions with respect to the morphological inter-relationships of the various ganglia. Thus, in the lateral chain of ganglia we find the cells on the course of the pilo-motor nerves, splenic nerves, and some vaso-constrictors (to surface of trunk). In the collateral chain are found the cells of many vaso-constrictors, of the nerves to sweat glands, salivary glands, of the inhibitory fibres to the alimentary canal, and of the cardiac accelerators, whilst in the terminal ganglia are placed among others the cells on the cardio-inhibitors, on the motor fibres to the lower part of the intestine and bladder, on the inhibitory fibres to the external genital organs, etc.

It is also of value to compare the different positions of the cells for analogous fibres to different organs. Treating the vaso-constrictors in this way we see that the cells are placed for the trunk in the corresponding lateral ganglia; for the upper limb in the ganglion stellatum; for the lower limb in the sixth and seventh lumbar, and first and second sacral; for the tail in the coccygeal ganglia; for the stomach in the cœliac ganglion; for the small intestine in the superior mesenteric; for the large intestine and rectum in the inferior mesenteric; for the external genitals in the

sacral ganglia; for the head in the superior cervical ganglion; for the submaxillary and sublingual glands in the superior cervical ganglion, etc.

The cells on the vaso-dilator fibres are placed in the superior cervical ganglion for the gums and lips, in the hilum of the gland for the submaxillary, near the viscus for the rectum or external genitals, etc.

The cells for the motor fibres of the upper part of the alimentary canal are in the ganglion trunci vagi, for the lower part, on the course of the fibres near the viscus. The cells on the inhibitory fibres of the upper part of the alimentary canal are in the cœliac or superior mesenteric ganglia, for the lower part in the inferior mesenteric ganglia or along the course of the colonic nerves or hypogastrics.

T. Gregor Brodie.

NOTES ON PARASITES.

I.

AMONGST the many doubtful points which have exercised the minds of those Zoologists who work at the parasitic worms, none has caused a greater divergence of opinion that the question of the existence or non-existence of an external epithelium. Since Rindfleisch and shortly afterwards A. Schneider, some thirty years ago, denied that such a layer existed, hardly any two writers have agreed as to the nature of the skin of Cestodes and Trematodes. All, however, have recognised the existence of a cuticle, but as to its nature there were almost as many opinions as there were writers. Rindfleisch and A. Schneider regarded it as the basement membrane of a lost epithelium, and this view was adopted by Leuckart and consequently gained a wide acceptance; other writers, however, held that the cuticle was itself the external epithelium which had become much modified and had lost all trace of cells and nuclei.

The recent researches of Professor Blochmann[1] of Rostock have done much to clear up this and many other doubtful points in the histology of the Cestodes and Trematodes. These researches have been largely facilitated by the employment of Golgi's method of staining and by the use of the Iron-hæmatoxylin staining fluid: they were chiefly carried out on *Ligula monogramma*, though twelve other species of Tape-worm and many Trematodes were also investigated.

Blochmann begins his paper by pointing out that if there is no external epithelium we must invent a new name for the cuticle, since it is of the essence of a cuticle that it should be formed from the free ends of epithelial cells; secondly, that external unicellular glands such as are common in Trematodes and also occur in Cestodes, though less frequently, are as a rule produced by the modification of

[1] *Die Epithelfrage bei Cestoden und Trematoden*, Hamburg, 1896.

some of the cells of an epithelial layer; and finally that absorption, which presumably takes place all over the body of Tape-worm, is usually in other animals effected by an epithelium. All these statements make it probable that such an epithelium exists, and Blochmann's preparations demonstrate its existence in the parasites in question, although in a somewhat modified form.

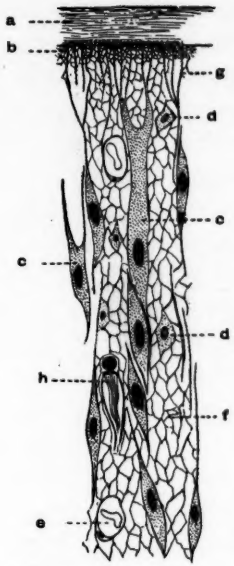

FIG. 1.—Transverse section through the outer part of the body wall of *Ligula monogramma* × 800. After Blochmann. The muscles have been in all cases omitted.

a, Cuticle.
b. Basement-membrane composed of close network of fibrils.
c. Epithelial cells.
d. Branching cells of parenchyma.
e. Cell of parenchyma containing a calcareous body.
f. Parenchymatous network.
g. Processes of epithelial cell terminative in swollen ends in the cuticle.
h. Flame cell of excretory system.

The body of a Cestode such as *Ligula* consists of a parenchyma or ground-substance (Fig. I. *f*) of the nature of connective tissue in which lie embedded the various organs, and which is traversed in various directions by muscular and nervous strands. According to Blochmann the external epithelium has to some extent sunk into this

parenchyma so that we do not find a sheet of contiguous epithelial cells on the inner side of the cuticle, but, instead, a thin layer of the parenchyma which in common with other authors he calls the basement membrane (Fig. I. *b*). Situated below this, though at slightly different levels, are a number of spindle-shaped cells with well-marked nuclei, these represent the external epithelial layer of other animals (Fig. I. *c*). Although the bodies of these cells are separated from the cuticle by the basement-membrane mentioned above, they have not lost their original connection with the external surface, but send up fine processes, often several from one cell, which pass through the basement membrane and terminate in the cuticle (Fig. I. *g*). The lateral separation of epithelial cells from one another which is here seen to be due to the intrusion of the parenchyma is paralleled in the case of the leech, where the connective tissue, often carrying with it minute blood-vessels, penetrates between the cells of the ectoderm. This feature is particularly well marked in preparations made from the body wall of a leech which has recently enjoyed a full meal.

The parenchmya of Cestodes, like other connective tissues, consists of cells and a ground substance. The cells are very richly branched (Fig. I. *d*), their finer ramifications stretching through the body in all directions, surrounding all the organs and often accompanying for some distance the muscle fibres. Their processes anastomose with those of other cells such as the epithelial cells and thus the parenchyma cells are in a position to play a large part in the nutrition of the parasite. They secrete the ground substance which they throw off in the form of fine membranes and strands forming a network in the meshes of which is a slightly coagulable, non-corpusculated fluid. This network penetrates everywhere between the epithelial and other cells, it surrounds the muscle fibres and even accompanies the branches of the nerve-cells as far as the cuticle where however the nerve fibres end freely. Certain of the cells of the parenchyma have become specialised to secrete the calcareous bodies (Fig. I *e*), and in these cases the secretion has much the same relation to the cell as the fat drop has to its cell in

adipose tissue. The nucleus of the cell can usually be seen on one side of the calcareous nodule.

There remains one point of great interest in Blochmann's paper, and that is that his researches render it extremely probable that the flame cells (Fig. I. *h*) of the excretory system are derived from the external epithelial cells and not as is often thought from the cells of the parenchyma. Careful preparations through the growing region of a *Taenia* show that the flame-cells are not formed by a parenchyma-cell fusing with the wall of one of the excretory canals, and so acquiring an outlet, but that they grow from these canals, pushing their way into the parenchyma. Thus Pintner's comparison between the flame-cell and a unicellular gland-cell, and between the excretory canal and the duct of the gland cell receives material support. This view of the external origin of the flame-cells is confirmed by the ectodermal origin of the excretory system in *Discocelis tigrina* described by Lang.

The interesting discovery of transverse commissures connecting the lateral nerve cords in Tapeworms has just been announced. Mr. Tower,[1] to whom we owe the discovery, studied two species of *Moniezia, M. expansa* and *M. planissima* both from the small intestine of sheep. He obtained the best results by using von Rath's preserving fluid, which stains the nervous tissue a greyish blue, and the muscles brownish, the connective tissue remaining lighter in colour than either.

Each lateral nerve cord swells out into a ganglion (Fig. II. *f*) at the posterior end of each proglottis, just behind the level of the transverse excretory canal. The ganglion consists of two kinds of ganglion cells, large and small, and gives off externally several fine nerves, of which one runs forward and is called by Tower the marginal nerve (Fig. II. *e*). The most important branches which arise from the ganglion are, however, a dorsal and a ventral one which traverse the proglottis and end in the corresponding

[1] *Zool. Anz.*, xix., 1896, p. 323.

ganglion of the other side (Fig. II. *a* and *b*), thus forming a complete ring round the body. The dorsal branch is further connected with the ventral by a small commissure situated just within the lateral excretory canals, which are thus in the posterior region of the proglottis surrounded by a nerve ring. Further, both the dorsal and the ventral commissures bear two small ganglionic enlargements (Fig. II. *g* and *h*) each of which gives off a small branch passing forwards and apparently ending—though there is still some

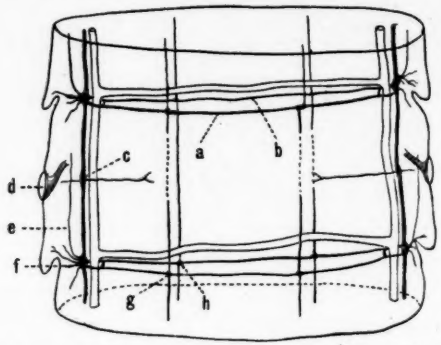

FIG. 2.—A diagram to illustrate the nervous system of *Moniezia* after Towers.
a. Dorsal commissure.
b. Neutral commissure.
c. Anterior lateral ganglion giving off internal and external genital nerves.
d. Genital pore.
e. Marginal nerve.
f. Posterior lateral ganglion.
g. Left dorsal ganglion.
h. Left neutral ganglion.

doubt as to this—in the corresponding ganglion of the preceeding proglottis.

Each lateral nerve cord in addition to the large ganglion at the posterior end of the proglottis (posterior lateral ganglion) also bears a small ganglion about the middle of the length of the proglottis near the genital pore (Fig. II. *c*). This anterior lateral ganglion gives off an internal genital nerve which supplies the ovaries and uterus and an external genital nerve which is distributed to the region of the genital orifice.

Tower's account of the nervous system in the Tapeworm proglottis is by far the most complete that we have

at present, but it must not be forgotten that others have seen at least one transverse commissure in each proglottis. Towards the end of his paper on the "Valves in the Excretory Vessels of Taenias" Kohler[1] describes in *Taenia expansa* a transverse nerve commissure connecting the lateral nerve near the posterior end of each proglottis. This commissure corresponds in position with the dorsal one in *Moniezia*.

Riehm and Zschokke have also described nerves passing transversely from the lateral cord, near the posterior end of the proglottis, towards the interior, but they failed to trace them right across, and in fact in the species they worked at the commissure may be incomplete.

ARTHUR E. SHIPLEY.

[1] *Zeitsch. wiss. Zool.*, vol. lvii., 1894, p. 385.

TERATOLOGY IN MODERN BOTANY.

MALFORMATIONS have long played an important part in botanical literature. On the one hand, every variation from that which we recognise as the regular form (which, on that account, is naturally regarded as the normal one) excites our interest, and on the other hand, we are enabled to obtain, by the study of these malformations, a deeper insight into the homologies of the organs, and especially those of reproduction of the higher plants. As I have dealt with this point elsewhere[1] I will not enter further into it here. For this period of Teratology belongs essentially to the past. The present has turned its interests to other questions. We ask rather now, what gives rise to these malformations, and what is their bearing upon the great problems of the origin of the organic forms?

In endeavouring to indicate shortly the most important contributions which have been made to the solution of these questions, I must lay stress upon the fact that it is not possible to define exactly what constitutes a malformation. No line of demarcation can be drawn between malformation and variation, though one would be inclined to lay it down as does Darwin,[2] that "by a malformation is understood any important modification of the structure of such a kind as to be disadvantageous or even useless to the species".

I.

How do malformations arise?

In attempting to answer this question, we encounter a serious difficulty at the very outset. Whilst we see that on the one hand they may be caused by definite external lesions, on the other there is a mass of evidence to show

[1] See "Entwickelungsges. d. Pflanzenorg., *Schenk's Handbuch*, iii., 1.

[2] *Entstehung der Arten*, p. 63, German translation.

that malformations may be hereditarily transmitted, that is to say, they may proceed from internal causes with which we are unacquainted. Instances of the latter kind have been partially known for a long time. It is a matter of common knowledge that the doubling of flowers may be perpetuated by seed, as may also the remarkable appearance of peloria in many plants (see Darwin, *Variation of Animals and Plants*), and even that in some cases constant races have been obtained which always produce certain malformations. This is the case in *Celosia cristata*, the well-known Cocks-comb. In the plants with which I experimented, my experience was opposed to that of other authors, for I found that the transmissibility of the fasciation by heredity is absolute. Even when I cultivated the plants in sterile sand, they always exhibited this phenomenon, even in the second generation.

Transmissibility by heredity, at any rate partial, may be assumed for all such malformations as arise spontaneously. Evidence in favour of this is afforded by the investigations of De Vries.

1. *Fasciation.*[1]—De Vries was able to demonstrate the hereditary transmissibility of fasciation in eight plants, though it was never so absolute as to be exhibited by every individual, but still the fact that it did occur was plainly shown. As an example may be taken *Crepis biennis*, in which fasciation was shown in the radical inflorescences

in the second generation in - -	30 per cent.
in the third generation in - - -	40 per cent.
in thefourth generation in - - -	30 per cent.
in the fifth generation in - - -	24 per cent.

Sometimes, too, a generation may be missed. Thus the seed from two fasciated flower-heads of *Taraxacum officinale* when sown gave, in the first year, only normal individuals, but in the second year the same plants showed ten fasciated inflorescences, and this increased to about 30 per cent. in later generations. External influences are

[1] De Vries, "Over de erfeligskheid der fasciatien," *Botan. Jaarb.*, Dodonala, 6, Jaarg., 1894, with résumé in French.

apparently of considerable importance. Only well-grown and well-nourished specimens showed the fasciation, and this agrees with facts to be referred to later.

2. *Forced twisting.*[1]—By "forced twisting," A. Braun understands the form which climbing-plants may exhibit, as a consequence of the distorted growth of the leaves in a spiral line of but little extensibility. This may occur as an abnormality in plants whose leaves are normally disposed in whorls, the leaves taking up a spiral position, growing awry at their bases, and so forming a wreath around the stem.

As the stem elongates, it is forced to unroll this spiral as far as possible, and turns itself in the opposite direction.

By observations made upon a large amount of material De Vries was able to demonstrate the correctness of Braun's views of forced twisting. The only specimens previously available had been those accidently found in a wild state. As soon as it was proved that forced twisting was hereditary, it became possible to procure numerous examples for purposes of investigation, and also to ensure the production of the abnormality. It was then found that weak seedlings give less prospect of well-marked specimens of forced twisting than strong and well-manured ones, in which, moreover, other malformations, such as increase in the number of cotyledons, fasciation, etc., are more apt to occur.

3. *Hereditary Sterility in Indian Corn.*[2]—In cultivating Indian Corn some of the plants were found to be completely sterile, and unbranched. In this case too, when heredity is in question, the relation must be precisely the same as in plants with double flowers, themselves sterile, but descended from single-flowered specimens, which latter tended to produce double-flowered offspring. An almost sterile plant, the spikes of which bore only very small grains was selected, and 19 per cent. of the offspring proved

[1] De Vries, "Monographie der Zwangsdrehungen," *Pringsheims Jahrb.*, xx.; and "Eine Methode Zwangsdrehungen aufzusuchen," *Ber. der. d. Bot. Gesellsch.*, xii.

[2] De Vries, "Steriele Mais as erfelijk ras," *Bot. Jaarb.* Dodonala, 1890; and "Over steriele Mais Planten," *ibid.*, i., 1889.

to be quite sterile, whilst of the offspring of other, more robust examples, sterility occurred in only a very few cases.

The experiments of Heinricher[1] must, lastly, be mentioned. He found that a second whorl of stamens which is normally absent when it did occur could be hereditarily transmitted. The precise form of the members of this whorl is, indeed, subject to great variation. The stamens are sometimes stunted, at others fully developed, sometimes they were replaced by staminodes, with or without pollen sacs, at other times they were reduced to mere scar-like structures. Complete fixation, *i.e.*, the cultivation of stocks yielding only six-stamened flowers has not yet been attained. A point of special interest is that flowers also occurred in which the inner perianth whorl was constructed in exactly the same way as the outer one, so that the form of flower in this case presented a great variation from the normal one, and might perhaps be regarded as an exaggerated reversion to an ancestral type.

II.

On the other hand, a number of cases are now on record in which malformations have been successfully produced by artificial means. We do not include in this category such appearances as result from insufficiency of light, conditions of temperature, and so on. The lower plants, especially the moulds, have proved to be particularly adapted for these observations.

Raciborski has recently produced interesting malformations in *Basidiobolus ranarum*.[2] This mould consists normally of cells containing a single nucleus, which are cylindrical in form and arranged in rows. The fungus is one which can be easily cultivated. If cultures be made in 10 per cent. Glycerine solution, and kept at a somewhat high temperature (30° C.), there are very often developed (though all the cells do not react alike) giant-cells of 60μ in

[1] Versuche über die Vererbung der Rückschlagserscheinungen bei Pflanzen," *Prings. Jahrb.*, xxiv.

[2] M. Raciborski, Ueber den Einfluss äusserer Bedingungen auf d. Wachsthumsweise d. *Basidiobolus ranarum*.

diameter which contain numerous nuclei, and between these latter in some cases delicate walls are formed. As the concentration of the culture-medium is increased the cells keep on diminishing in length and approach the spherical form, whilst the walls assume, with increasing frequency, an oblique or even longitudinal direction instead of a transverse one, this never happening under normal conditions. We here meet, apparently, with fundamental disturbances of growth; the giant-cells are no longer capable of multiplication, but eventually die out. Other abnormalities will not be referred to here, except to state that by cultivation in 1 per cent. ammonium sulphate or 10 per cent. ammonium chloride *Basidiobolus* may be compelled to pass through a "Palmella stage," which is unknown in the case of any other mould. It isolates itself as spherical cells with thick walls, and these free themselves from the old cell-envelope. The interference with development is clearly more limited in this instance than in that of the giant-cells above described.

Similar results have been obtained in the case of some algæ; in these, too, abnormalities may be produced by the composition of the culture-medium, especially as regards its concentration, though they do not go so far as in *Basidiobolus*. Thus, Chodat and Huber found[1] that in *Pediastrum Boryanum* the formation of daughter-colonies does not occur in concentrated culture-media, and the cells sometimes become metamorphosed into large "hypnocysts"; Richter[2] has also seen abnormalities occur in other freshwater Algæ when cultivated in salt solution.

In passing on to the Phanerogams I would repeat, in the first place, the words with which a distinguished investigator on the etiology of malformations, Peyritsch, opens his treatise upon the origin of the formation of peloric flowers. He says: "In studying the cause of the formation of peloric flowers, and especially in reference to modifications of structure, two points must be kept in mind. One refers to *causation;*

[1] "Recherches experimentelles sur le *Pediastrum Boryanum*," *Bull. Soc. bot. Suisse*, 1895.

[2] Ueber die Anpassung der Süsswasseralgen an Kochsalzlösung," *Flora*, p. 4 *ff.*, 1894.

and it implies that although in many cases the agent is an external one, there is an internal factor also, that is to say, a predisposition to the production of the anomaly. One may convince one's self by experience that all individuals of a given species do not react to an external influence of an unfavourable character in the same way at all times, nor is the capacity to vary or to appear under abnormal forms, to suffer from disease, equally present in all in the same fashion."[1] And the experiments of De Vries, above referred to, lead to the same conclusion.

For our present purpose it is indifferent whether peloric flowers be regarded as malformations or as examples of "reversion to type". Without doubt the radial forms of inflorescence represent an earlier type of flower-disposition than the dorsiventral (zygomorphic) flowers which are normal to the plants referred to.

As regards the etiology of peloria it is known that when flowers are developed at the apices of stems the remainder of the flowers upon which are zygomorphic, these apical flowers are, almost without exception, radial (peloric), but laterally situated flowers *may* also develop as peloric ones. The influence of position upon zygomorphy is thus here unmistakable, though the attempt to prove this by strict experimental methods is an exceedingly difficult task. Thus, although Hoffman[2] endeavoured to produce peloric flowers in *Achimenes grandiflora*, *Salvia Horminum*, *Gloxinia speciosa*, and others, the negative results of these experiments would seem to have been a foregone conclusion, made, as they were, by causing the flower-buds to assume a vertical position artificially. By the time that the flower-buds, zygomorphically arranged, are amenable to treatment, their development has advanced to such a point that it is useless to expect any modification of importance to take place. Hence Hoffmann's experiments are scarcely capable of being employed for critical purposes, numerous though they were.

Peyritsch, in his work already referred to, endeavoured

[1] *Denkschriften der K. k. Akad. Wien*, bd. 38, 1878.

[2] *Botan. Zeitung*, p. 625, 1875.

to arrive at the immediate cause of the formation of peloria by other means. Starting from observations made upon wild plants he asked himself whether the formation of peloria might not be determined by a change in the conditions of life. Experiments with *Galeobdolon luteum* and *Lamium maculatum* seem to indicate that this is actually the case. These experiments, it is true, leave many important questions unsolved, but I mention them the more readily in this place since an extended repetition of them is greatly to be desired.

In their natural habitat the Labiates just mentioned grow in the shade of other plants. If the latter be removed, as, for instance, by the clearance of wood in forests, many peloric flowers, accompanied by other abnormalities, make their appearance. It is thus reasonable to assume that the increase in the intensity of light acts as the proximate cause of these malformations, and the view that changes in the conditions of life cause plants to vary is thus clearly supported. Plants were then exposed to a stronger illumination, and although control-experiments, made by dividing the stocks and placing a portion of the plants in normal (shady) situations, were unfortunately omitted, it was found that some specimens failed altogether to develop flowers; in one case the time of flowering was altered, and the flowers were borne on shoots which do not normally carry them, whilst three examples produced terminal peloric blossoms. Two specimens were nearly normal, but even in these the proportion of the floral leaves was abnormal in one flower.

In the following year the abnormal appearances were less marked. The plants seemed, so to speak, to have grown accustomed to their new conditions of life; and although the production of flowers was lessened, this was doubtless due to the unfavourable influences operating upon the growth as a whole. Similar anomalies occurred in *Lamium maculatum*, though, as in *Galeobdolon*, these never extended to the whole number of plants. Abnormalities occasionally occurred in the vegetative region, but all the plants did not react alike. It must be mentioned here, and

indeed the fact has already been referred to, that in a number of plants, *e.g.*, *Digitalis purpurea*, the tendency to the formation of peloria is transmissible by seed, and Peyritsch relates a similar case in *Leonurus cardiaca* among the Labiatæ. In *Galeobdolon* and *Lamium*, however, the tendency (which must be here regarded as a latent disposition) to the formation of peloria only shows itself when special conditions of life call it forth. In this connection an example may be mentioned which does not indeed belong strictly to teratology, but which shows that there may be present in a plant two different organ-forming tendencies, of which the one is in a latent condition at a certain stage in the life-history of the plant, but may be brought into action by the operation of external factors. Many swamp-loving monocotyledons first produce lanceolate primary leaves,[1] whilst later they bear more highly developed leaves with stalks and blades. A plant of *Sagittaria natans* or *Eichhornia azurea* may, however, be compelled to repeat the formation of the simple leaf by merely placing it under unfavourable conditions, by cutting the roots, for example, or by immersing them in distilled water. The power to form these early simple leaves is thus proved to have been still latent, and although the plant had long been producing other leaves, stimulus from without brought this power into activity again.

In a similar way we can explain the fact that fasciation may be artificially produced by causing the sap to pass rapidly and with increased intensity into a lateral bud which would normally receive but a small quantity of nutriment may be readily produced in some annual plants (*Phaseolus multiflorus*, *Vicia Faba*) by cutting off the main axis above the cotyledons. The axillary buds frequently then become fasciated instead of developing normally. In the same way I was able to cause the simple primary leaves of *Vicia Faba* to develop into foliage leaves, or into such intermediate forms between foliage and primary leaves as any teratologist would recognise as malformations, and in experiments in-

[1] See Goebel, *Pflanzenbiol. Schilderungen*, vol. ii.

stituted by A. Mann at my suggestion, he succeeded partially in effecting a like transformation in *Pisum sativum* in all these cases the effect was due to definite material causes, and we are justified, therefore, in assuming that a similar cause operates when the malformations are caused by animals or by parasitic moulds. I confine myself to the former, since such causes have received far less attention than those of the latter class.

The experiments of Peyritsch on the production of double flowers and other variations of structure by artificial means are of special interest.[1] Unfortunately the death of the investigator has rendered it impossible for him to give the full results of his experiments in detail, and we possess only the short communication referred to along with another[2] in which the author showed that by infecting species of *Arabis* with species of *Aphis*, chloranthy may be artificially produced, provided that the development of the buds selected for the operation be not too far advanced. The chloranthy was accompanied by interference with the development of the sexual organs, the pollen in particular being rudimentary, and apparently incapable of performing its function.

More pronounced malformations were produced by the infection of other plants, *e.g.*, some Valerianaceæ and Cruciferæ, with *Phytoptus*. These consisted partly of abnormalities in the leaves, and partly in various kinds of double and proliferating flowers. The first group generally consisted in the arrangement of the teeth of the leaves in a comb-like manner on leaf flaps which projected considerably beyond the general outline of the leaf. In *Centranthus calcitrapa* this appearance often took the form which Masters in his *Vegetable Teratology* (p. 445), describes as "Enation of leaf-organs".

In the inflorescences of Cruciferæ the bracts to the flowers which are usually absent (aborted) in this order

[1] "Sitzungsber. der Kais. Akad. d. Wissensch. in Wien," Bd. xcvii., 1888.

[2] "Aetiologie der Chloranthien einiger Arabis-arten," *Pringsh. Jahrb.*, xiii., 1.

frequently appeared in connection with several of the flowers and resembled small foliage-leaves in form and texture. Again, the doubling of the flowers occurred in the most various ways, all intermediate stages between the conversion of odd stamens and carpels into petals, and complete doubling being represented, and some flowers further had double, some treble corollas and calyces. And besides this, fresh shoots were also observed in the interior of some of the flowers.

All these effects were produced by inoculation with a parasite, a *Phytoptus*, which occurs in aborting buds of *Valeriana tripteris*. The degree of metamorphosis was not the same in all cases, but varied with the strength of the infection, and with the sensitiveness of the plants.

Two points in these experiments appear to me to be of special significance. The one is the fact that, as in the formation of galls, the malformations are due to a direct action on the part of the parasite, and secondly, that in the process there is no formation of new organs, but rather an interference with any such formation.

This statement may appear at first sight too sweeping, wanting in clearness, and doubtful, but I consider it as representing the correct position, and I will go on to support it by some examples. When a flower becomes green the foliage-leaves which supersede the petals, stamens, and so on, take the form of the ordinary foliage-leaves of the plants, *e.g.*, in *Drosera* it is even found that the chloranthic blossoms have upon their leaves the characteristic tentacles. The chloranthy is, indeed, not always perfect, and the forms of the leaves which result from it are then simpler, but the extreme cases give very clear indications of the general nature of the process. Moreover, when flowers become double and new petals are formed, the latter have the same form as the ordinary ones, in accordance with the principle just laid down. The malformation consists in an abnormal metamorphosis, and to a certain extent in *pot pourri* of the various organs. But as in the development of galls no histological components which are absent from the plant make their appearance, so, in these malformations,

no new morphological element is to be found. The *combination* of already existing properties is new, but the properties thus combined remain themselves constant, like the fragments of coloured glass which give rise to the changing pictures of the kaleidoscope. Malformations resulting in the formation of compromises between two organs are the very frequent consequence of this, thus Peyritsch has observed in *Valeriana* all intermediate stages *between* bracts and pappus-rays instead of bracts only, and the same between bracts and petals.

If then nothing new arises during such malformation, but only another combination of parts already present, we are justified in concluding that it is necessary to be cautious in assigning phylogenetic significance to malformations as has very often been done. Admitting that many of the latent capabilities which exist in plants are called into action in an augmented degree by malformation processes, the question is only one of the revelation of something which was really existent though in an attenuated condition, and not of a change in the organs as a whole. This occurs when, for instance, leaflets appeared instead of ovules in chloranthic flowers. The characteristics of ovules, the embryosac, and so on, have disappeared. But, on the other hand, when the *bracts* of the inflorescence of a Crucifer, for instance, are developed, this may, upon comparative grounds, be regarded as a reversion to type. The same is true of the fact observed by Treub and others, that when gall-formation occurs in the flower-heads of *Hieracium umbellatum*, Calyces in all stages from the normal pappus of the flower to the occurrence of five separate green leaflets with regular venation were found. But such an inference can only be justified by comparison with allied forms, since it is probable that there are also latent tendencies which were never developed in the ancestral forms.

Thus, in *Selaginella pentagona* A. Braun and Strasburger have noted remarkable gall-formations, externally resembling bulbils. These have six rows of similarly formed leaves, whilst, as is well known, the leaves of Selaginella are nor-

mally arranged in four rows, the leaves in two of the rows being much smaller than those in the other two rows. An arrangement of leaves such as is exhibited in these gall-bearing shoots (which are inhabited by the larva of a Dipterous insect) is never found in Selaginella under other circumstances. The bulbils grow with a triangular pyramidal apical cell. The first stages in their development are unfortunately unknown, but they probably begin as outgrowths on young shoots as a result of the irritation produced by the larva.

A similar instance is afforded by the singular "witches brooms," which are formed upon the leaves of *Pteris quadriaurita*, as the result of the action of a mould, *Taphrina cornucervi*. These are adventitious shoots with misshapen leaves; adventitious shoots do not normally appear upon the leaves of the plant in question.

The malformations, resulting from the action of animals already alluded to, lead us to glance at the latest observations upon the origin of galls. It is not surprising that these curious structures should have attracted attention at an early period. We see here that, as the result of irritation applied by an animal, there arises a new growth which is admirably adapted to afford food, dwelling, and shelter to the creature therein developed. What is the nature of this stimulus? In the opinion of Lacaze-Duthiers,[1] with which Darwin and Hofmeister also concur, a poisonous substance is introduced by the insect when laying the egg by means of its ovipositor, and that this gives rise to the formation of the gall. It is evident that the irritation to which the parent insect gives rise presupposes a power of responsive action; the virus of *Cynips rosæ*, for example, is destitute of action upon the oak, which nevertheless so readily produces galls under appropriate stimulation.

As has, however, been shown by the well-known entomological researches of Adler, the theory enunciated by Lacaze-Duthiers cannot be regarded as trustworthy. In the department of botany our knowledge of the formation

[1] "Recherches pour servir a l'histoire des galles," *Ann. Sci. Nat. Bot.*, 1853.

of galls has been greatly added to by Beyerinck.[1] It was found that in galls produced by Cynipidæ, the stimulus which determined the gall-formation did not proceed from the parent, but from the larva. The influence of the latter is exerted even whilst still contained within the egg as is proved by the simple fact that in many cases the eggs are deposited on the surface of the young organs of plants and cemented there, and are then surrounded with a wall by the adjacent tissue. This can only be explained upon the supposition that the larva secretes soluble substances, and that these enter the tissues of the plant. Again, the larva has often been removed from the growing tissue which is being converted into the gall, and indeed in some cases has been separated from the growing tissue by dead tissue, without influence upon the growth of the gall. This shows that the case with which we have to do is not one of propagation of the irritation, assisted by the living protoplasm of the host. Moreover, since the action is a slow one and proceeds from the larva, it may be arrested by killing the latter. Since their growth is interfered with at those points of the young tissues which are in immediate contact with the animal, there is formed a chamber which is always lined with nutriment at the disposal of the larva. As regards the theory of gall-formation, the fact discovered by Adler is of great importance, confirmed as it has been by Beyerinck, that upon one and the same host, the oak, the various forms of a single species of gall-insect produce various galls. The female insects of *Dryophante folii*, for instance, emerge from their galls upon an oak-leaf in November or December. They immediately look for a bud, a "resting eye," and deposit an egg upon its vegetative point, a small violet-coloured bud-gall resulting, which, before the connection was known, was ascribed to a gall-insect known as *Spathegaster Taschenbergi*. The males and females of this species leave their dwellings in May, and the fecundated female insects deposit their eggs in the veins of young oak-leaves and thereby give rise to the leaf-galls with which we started.

[1] "Beobachtungen über die ersten Entwickelungsphasen der Cynipidengallen," Amsterdam, 1882.

The two galls differ both in form and in histological structure. Does this arise from the fact that the substance secreted by the parthenogenetic eggs (which substance determines the gall-formation) is a different one from that formed by the impregnated eggs, or is it due to a difference in reaction between the vegetative point and the leaves? The reply to this question is, in my judgment, of far greater importance than the investigation of apical cells and other minute histological details on which so much labour is being expended.

We have already referred to the admirable adaptation of the galls to the requirements of the larvæ, and a point of special interest is that the animal is also protected from enemies during its development, partly by mechanical means, partly by chemical ones (especially the abundant formation of tannin), though the fact that this protection is by no means absolute is shown by the frequent attacks to which the galls are subjected.

The protection required is in other cases effected as the result of the irritation caused by the larva in the shape of the formation of roots which overgrow the larval chamber, and by becoming fused together forming a close living mantle. This is the case with the gall which *Cecidomyia Poæ* causes upon *Poa nemoralis*.[1] The roots in this case arise at points at which they normally are never found. Here the irritation which leads to the formation of the gall proceeds from the larva, which attaches itself firmly to the surface of a still-growing internode; fold-like swellings first appear at a considerable distance on either side of the larva, and the roots arise from these swellings, and may be made to develop into normal roots if the gall be used as a slip or cutting. The behaviour of *Nematus capreæ* however shows that the gall is not always formed *entirely* as a consequence of the action of the larva. The old theory of Lacaze-Duthiers here applies, the development of the gall depending upon the substance which is introduced into the young leaf with the egg from the poison bag. This is clear from

[1] Beyerinck, *Bot. Zeitg.*, p. 305, 1885.

the fact that every wound caused by the saw of the insect gives rise to a gall, even when no egg is laid, and further, that the artificial destruction of the egg does not prevent the formation of the gall, the development of the egg determines only the size of the gall.

In concluding this short account of the latest researches into the formation of galls, two points alone need be adverted to. The one is, that in the anatomical structure of gall generally, no new tissue-components appear other than those which the plant attacked already possesses, though they exist under other conditions as regards situation and distribution. The other is, that all the more highly-differentiated galls spring from young tissues still in course of development, these being caused to assume abnormal structure as the result of the action of the gall-insect.

III.

Certain general conclusions which arise out of the preceding facts have already been alluded to, and we may here shortly refer to the theoretical considerations to which they have led. The chief of these is Sachs's theory of "material and form"[1] which has been specially employed with reference to malformations.

Sachs starts with the assumption that the differences in the forms of the organs of plants depend upon differences in their material components, and that the variations in the organic forms result from variations in the processes of nutrition. Thus the substances which give rise to the formation of a foliage-leaf are different from those which lead to the formation of a carpellary leaf. If this be so, the causative action of the so-called morphological processes may be admitted, just as in the instance of the morphology of a crystal. We can then form a mental picture of the way in which it happens that in malformations, one organ so frequently appears in the place of another, or that the relative forms of the two organs are commingled in the

[1] *Gesammte Abhandl. über Pflanzenphysiologie*, J. v. Sachs, ii., 1156 ff.

strangest fashion, just as are the peculiarities of two different species in their hybrids.

The malformations caused by animals show us, as a matter of fact, that the development of organs is modified by material influences, although, as has been said, the range of those modifications is naturally limited by the peculiarities of the particular plant. The fact that they are of such frequent occurrence in the flowers, and relatively rarely are found in the roots, for example, may be due to the following peculiarities :—[1]

1. The organs arise at the vegetative point of the inflorescence in rapid succession, and usually in considerable number, close above and by the side of each other.

2. There are thus formed at short intervals organs of varied structure, *e.g.*, petals, stamens, etc.

3. Comparatively slight disturbances would thus suffice to call forth changes in the arrangement as the organ-forming materials are supplied, since the normal development of parts of so complicated a character can only occur when the supply of material and the phenomena of cell-division occur with almost mathematical exactitude. If, for example, a few molecules of the material which gives rise to the growth of anthers were diverted to the right or left to the extent of the thousandth of a millimetre, or were to be delayed or accelerated upon their journey in the apical region of the inflorescence, the characters of a stamen might be partially assumed by a petal or a carpel.

During my researches into the development of double flowers,[2] I was led to the conclusion that Sachs's theory offers really the simplest expression of the facts. In all these cases the question is one of increase in the quantity of the materials out of which the parts of the flower are formed. This finds expression at one time in the cleavage of the normal layers of the parts, at another in the appearance of new whorls, and again, in the conversion of

[1] Compare Sachs, "Ueber Wachsthumsperioden und Bildungsreize," *Flora*, p. 217, 1893.

[2] Goebel, "Beiträge zur Kentniss gefüllter Blüthen," *Pringsh. Jahrb.*, xvii., p. 207 ff.

other whorls in the flowers into petals, and with these disturbances there are connected numerous and far-reaching ones in the structure of the composition of the flower as a whole.

Beyerinck [1] has been led to similar conclusions to those of Sachs upon the question of the formation of galls. He assumes that the substance secreted by the animal possesses the character of an enzyme, and that there are "enzymes of growth," which so effect the protoplasm of host that gall-formation results. Beyerinck assumes similar enzymes of growth in normal development of organs, only that in this case they are produced by the protoplasm of the plant itself. Since these enzymes must apparently be different for each organ, his theory very nearly approaches that of Sachs.

We must, however, be satisfied with this short account of the general question. And although the preceding exposition may be far from affording an exhaustive account of the matter, it may yet suffice to show that whilst the object and method of teratology in modern botany have changed, the subject has not lost anything of its interest or importance, rather the reverse.

K. GOEBEL.

[1] *Botan. Zeitg.*, 1888.

THE NERVOUS SYSTEM OF CŒLENTERA.

SINCE Oscar and Richard Hertwig published their extremely valuable monograph on the sea-anemones, when the nervous system both in the ectoderm and the endoderm of these animals was for the first time accurately described, a series of important papers has been published both at home and abroad confirming their general results and extending them to other groups of Cœlentera. The anatomical details of the nervous system of a group of animals which must still be regarded as the most primitive of all Metazoa naturally excites the interest of all zoologists and physiologists. The complicated nerve ganglia and cords of Chætopoda, Arthropoda, Mollusca and Vertebrata are in nearly all cases situated in the mesoblastic tissues of the adult. The teaching of embryology points undoubtedly to the ectoderm or epiblast as the source from which this nervous system is derived. Therefore must we look to those animals which do not possess any mesoblast at all if we wish to learn more about the original form the nervous system of animals possessed.

In the higher Metazoa the greater part of the nervous system is not difficult to discover.

The greater ganglionic enlargements, and the bundles of nerve fibres forming nerve cords from which the finer branches pass to the muscles and the organs of sensation, stand out clearly from the surrounding tissues. But in some forms, such as Nemertine worms, Platyhelminthes and in the embryonic stages of many others, including several Vertebrata, the main trunks of the central nervous system not only give off definite nerve fibres to definite organs or tissues but are connected with a loose, spongy plexus of fibrils and cells which spreads through the tissues in a manner that it is difficult to fully map out.

In most cases such as Palæonemertines, Nematoda, Tadpoles, etc., this plexus is situated immediately below but continuous with the ectoderm, and it is reasonable to

suppose that it is homologous with the ectodermic nervous system of the Cœlenterates.

Regarding the nervous systems of these animals from a general standpoint, we notice that they differ from the Cœlenterates in two particulars. Firstly, in the presence of certain ganglia are tracts of nerve fibres in addition to the subectodermic plexus of nerve cells and fibrils, and secondly, in the fact that the endodermic nervous system is either absent altogether, or else that it is so poorly represented that it has hitherto escaped observation. (The plexus of Auerbach and Meissner in the alimentary canal of Vertebrates may represent the endodermic nervous system, but so far as I am aware there is no embryological proof of this at present.)

The predominance of the ectodermic nervous system in the higher animals is readily accounted for by the fact that all the most important sensory impulses must originate in ectodermic tissues and the great muscles which move the body and limbs of the animal are derived from the somatic *i.e.*, the subectodermic layer of the mesoblast. The muscles of the splanchnic layer of the mesoblast which are moved by the endodermic nervous system—if such a system is really present—are comparatively slight, and the sensory impulses of the endoderm, although important physiologically perhaps, are general rather than special in character.

Two important questions have now to be considered. Firstly, do the plexus and the fibrils situated in the ectoderm of Cœlenterates really perform the same or similar functions as the epiblastic nervous system of the higher animals? And secondly, is there any direct or indirect histological communication between the ectodermic and endodermic plexuses?

In the consideration of the answer to the first question we must remember that the histological similarity of the tissues of two animals is not a conclusive proof that they perform the same functions. To prove that any system of cells and fibrils is nervous in function we must have physiological evidence that they originate, reflect, or transmit

nervous impulses. In the higher animals it is not difficult to obtain such physiological proofs of the functions of the nervous tissues but in most Cœlenterates where these tissues are extremely minute and diffused over a wide area the proof is not so easy to obtain.

A series of observations and experiments made last year by Hesse seem to afford the necessary proof of the nervous character of the ectodermic nerve plexus in certain Scyphomedusæ, and consequently mark a very important step in advance.

At the margin of the umbrella in these animals there may be seen a small number of very minute and extremely modified tentacles called the tentaculocysts.

These organs have been shown by Romanes and by Eimer to be the centres from which the impulses controlling the movements of the bell proceed, and from this fact, and others which it is not necessary for our purpose to refer to, they are frequently spoken of as the "sense organs" of the medusa. When all eight of the sense organs of an Aurelia, for example, are removed, the rhythmic contractions of the bell cease altogether, if one or any greater number are left intact the contractions continue. If the margin of the bell with one or more tentaculocysts be removed it continues to contract, whereas the remainder of the bell from which the margin has been removed ceases to contract. These and other experiments together prove that the nerve centres originating and controlling these contractions reside in the sense organs. Now on the inner, and in some genera on the outer, surface as well of the base of the tentaculocyst there is situated a pit, and it is a well-known fact that at the base of these pits there is a considerable thickening of the subectodermic layer of cells and fibres which is commonly called the "nerve sheath".

Hesse shows that the thickening of the subectodermic nerve plexus in each inner pit gives origin to several very much elongated bipolar ganglion cells, which run in very definite tracts. Passing from the sense organ immediately below the subumbrellar epithelium they form a bundle of fibres running in a radial direction towards the centre of the

bell. After a short course in this direction these elongated cells bend at right angles and form together with similar cells proceeding from other sense-organs a circular band of fibres, which completes the circuit of the bell. In connection with these circular and radial nerve tracts there are bundles of muscular fibres arranged in a regular and rather complicated manner, and there seems to be little doubt that the rhythmic contraction of these fibres causes the rhythmic contraction of the bell as a whole. It cannot be said that Hesse's observations on these histological points are altogether novel. Claus, Eimer, Schäfer and others have partially described them before, but with the help of more modern methods of research Hesse has been able to give us a more complete and satisfactory description than any of his predecessors.

Without referring to further details of the distribution of this important nerve plexus we may now, in view of the physiological experiments to be described, consider it to be proved that the so-called nerve sheath of the inner sensory pit of the tentaculocysts is continuous with bundles of fibres —or elongated bipolar ganglion cells ; that these fibres run radially from the margin and then circularly to form a broad tract, and that finally these tracts are confined to the subumbrellar aspect of the bell.

It can be shown that if semicircular incisions be made through the subumbrellar epithelium round each of the tentaculocysts, so as to cut through radial tracts, the effect is the same as if the tentaculocysts were entirely removed, that is to say, the rhythmic contractions cease. Moreover if the epithelium of the base of the tentaculocyst itself be severed the effect is the same. On the other hand if the epithelium on the upper side of the ball be cut in a similar manner and with it the subjacent mesoglœa the contractions continue, so long as the subumbrellar epithelium is intact.

These experiments prove then conclusively that the nervous impulses which stimulate and regulate the movements of a medusa traverse the subumbrellar epithelium only in definite directions, which correspond with tracts of

the cells and fibres previously described as nervous from histological appearances,

It is not probable that we shall be able to prove in a similar conclusive manner that the "nervenschicht" of the Hydroids and of the Anthozoa has the same function, but nevertheless these experiments give us much more confidence in the assertions that are made as to its nervous function.

Mention was made at the commencement of this essay that in sea-anemones and other Cœlenterates the nerve plexus is not confined to the ectoderm, but that similar cells and fibres may be found in connection with the endoderm.

The brothers Hertwig have described and figured this endodermic nervous system in the sea-anemones, but perhaps the most favourable Cœlenterate that can be readily obtained for its investigation is the Alcyonium.

This form consists of lobate colonial masses perforated by tubes—the polype cavities—passing from the surface, where they terminate in the mouths of the polypes, to the base of the colony. These tubes are lined by endoderm. The ectoderm is confined to the general surface of the mass and to the body wall, tentacles and stomodæum of the protrusible portions of the polypes. It would be impossible in such an essay as this to describe the details of the course of these two layers, but it will be sufficient to state that when compared with a Hydrozoan or a sea-anemone, the endoderm is in Alcyonium a very extensive and important tissue. The endoderm lining the tubes is provided with a considerable muscular layer — the muscles forming a cylindrical sheath immediately subjacent to the epithelium.

It is now fully recognised that when an Alcyonium is removed from the water or irritated in any manner in the water it is capable of contracting in bulk very considerably, and this contraction must be brought about by the cylindrical muscle sheaths expelling a portion of the water in the tubes.

The endodermic nervous system which, we may presume, governs these contractions, may be seen quite clearly

in fresh preparations stained by the Ehrlich methyl-blue method, in the form of a plexus of ganglion cells and branching nerve fibres.

This plexus is in connection with certain branching cells sparsely scattered in the mesoglœa, and it seems extremely probable that these in their turn are connected with the ectoderm, although technical difficulties have made it impossible to prove this point at present.

In the Hydrozoa and Scyphozoa the endodermic nerve system can only with much greater difficulty be discovered, and it probable that in the majority of these forms it plays a far less important part than it does in the Anthozoa.

In Klujostoma Hesse figures a marked endodermic nerve sheath on the outer side of the canal of the tentaculocyst. This sends short, tag-like processes into the mesoglœa in the direction of the outer sense pit. Corresponding with this the thickening of the nerve sheath of the outer sense pit sends tag-like processes into the mesoglœa. In the mesoglœa of the same region numerous small angular cells are to be seen differing in several peculiarities from the cells found in the mesoglœa of other regions. The conclusion seems to be irresistible that at this point there is established a communication between the endodermic and ectodermic nervous sheaths by way of these stellate cells, and the arguments by which Hesse seeks to prove that this is not the case are far from being conclusive.

Apart from this, however, the endodermic nervous system and its connections of the Hydrozoa and Scyphozoa have not yet been satisfactorily investigated and it is to be hoped that before long some one will with the new methods undertake a thorough investigation of the structure of the endoderm of these animals. The facts of the Cœlenterate nervous system which may now be considered to be established are these. That a plexus of fibres and cells occurs in both ectoderm and endoderm similar in structure and probably similar in function. In some Cœlenterates such as the Scyphozoa, the Ctenophora, many Hydroids, and the Sea-anemones, the ectodermic nervous system is the predominant one as it is in the Cœlomata, but in some of the

colonial Anthozoa, such as Alcyonium, it is the endodermic nervous system which is the predominant one. A communication exists between the ectodermic and endodermic nervous systems in the Anthozoa by way of a loose plexus of cells and fibres, but to what extent this also occurs in Hydrozoa and Scyphozoa we have at present but little evidence.

SYDNEY J. HICKSON.

PALÆOBOTANY AND EVOLUTION.

THE geological history of existing classes of plants is still very imperfectly known. The records of the vegetation of past ages are from the nature of the case exceedingly scanty, and it is only under special conditions that it has been possible for plant remains to leave traces of their existence in the stratified deposits of the earth's crust. The much greater abundance of fossil animals, and the better state of preservation of their hard calcareous, silicious, and bony skeletons, have enabled palæontologists to furnish valuable aids to the history of evolution. Some of these contributions from their readily perceived importance and exceptional interest, have long been familiar to every one possessing the most superficial knowledge of Natural Science.

From palæobotanists we have had various attempts to illustrate the progress of plant evolution by means of genealogical trees of the most comprehensive form, starting from a host of supposed algal remains in the older Palæozoic sediments, and culminating through various ramifications in the highest types of plant structure. The data on which it has thus been essayed to illustrate the manner of origin of existing classes of plants, are frequently valueless, and the evidence available hopelessly inadequate for so ambitious an object. In the majority of cases the building up of such imaginary lines of development has tended "to confuse fancy with fact, and to create mere confusion".[1] The acknowledged insufficiency and unscientific foundations of speculations on plant evolution, have tended to an attitude on the part of scientific investigators of extreme scepticism, and to a general mistrust of palæobotany as a factor of primary importance in phylogenetic inquiries.

Although, generally speaking, fossil plants are comparatively rarely found in a condition sufficiently satisfactory

[1] Huxley, *Method and Results*, London, p. 120, 1893.

for accurate determination and diagnosis, they have occasionally been preserved in a manner far more perfect than is the case with fossil animals. The hard parts of an animal may be found in a wonderful state of preservation, but the soft parts have at most left but a faint impression of their outline, and that only in a few exceptional cases. A well-known example of the impression of a soft-bodied animal is that of the Cambrian Medusa, *Medusites Lindströmi*, Nath., from the Eophyton Sandstone of Gothland. With plants, on the one hand, it is possible to investigate the minutest microscopical details in the structure of the most delicate tissues. Putting aside for the present all those records of extinct plants, which consist simply of structureless casts and fragmentary impressions, we have left a mass of material which has led to something more than vague suggestions and fruitless speculation. As the result of the examination of petrified vegetable fragments of the Permo-Carboniferous strata of England, France, Germany, and other countries, contributions have been made towards the solution of phylogenetic problems based on the most solid foundation of fact. It is notorious that those who confine their attention to living forms, have in a great measure allowed their interest to be restricted within the limits of existing organic types. Fossil and living plants have been treated by different methods, and looked at from entirely different standpoints. In recent years, however, botanists, as a whole, have begun to realise the importance of a logical attitude with regard to the unity of the past and present representatives of the vegetable kingdom. There are now, indeed, unmistakable signs of a more general recognition of the lessons to be learnt by means of the better methods of palæobotanical research, and this awakening interest in the investigation of extinct types is likely to be considerably extended. If we endeavour to take a comprehensive view of recent advances in botanical science, it is difficult to ignore the fact that there are few if any discoveries of more far-reaching and general importace than those furnished by palæobotanical investigations. The prospect in this field of work is a particularly

hopeful one, and cannot fail to attract the attention, if not the actual co-operation, of those interested in the broader problems of botanical research.

The examination of fossil organisms has not infrequently led to the recognition of certain characters suggestive of a combination of features now separated in distinct families. Even before the publication of the *Origin of Species*, the existence of generalised, synthetic, or prophetic types had been hinted at, and in more recent times the interest attached to such fossil forms has considerably increased. In searching for the ancestors of living forms we may sometimes arrive at a point where branching lines of affinity converge, and point back towards some generalised pre-existing stock. The recognition of any such synthetic forms, when based on trustworthy evidence, marks a great advance, and furnishes a far more valuable contribution to the history of organic evolution, than does the construction of genealogies which rest to a large extent on pure assumption, and appeal but little to the well-regulated scientific mind. It is true there are to be found in palæobotanical literature generalisations enough based on imperfect data as to the existence of supposed synthetic types; to refer to a plant which is imperfectly known and little understood, as combining in itself the characteristics of distinct groups, is often a convenient method of coming to a conclusion. Fortunately in not a few cases the evidence on which generalised forms have been described is as sound and conclusive as evidence can be.

No better illustration of such synthetic types can be described, than those recently dealt with in a most able manner in the pages of the *Philosophical Transactions* by the late Professor Williamson and Dr. D. H. Scott. In their memoir on the genera *Lyginodendron* and *Heterangium* the authors have contributed to botanical science results of exceptional importance, demonstrating in the clearest manner the possibilities of palæobotanical work when carried out on strictly scientific lines, and aided by a wide and accurate knowledge of the morphology of recent plants. We may best express the nature of those two Palæozoic fossil plants

by quoting the authors' words: "The view of the affinities of *Lyginodendron* and *Heterangium* which we desire to suggest is that they are derivatives of an ancient and 'generalised' (or rather non-specialised) Fern-stock, which already show a marked divergence in the Cycadean direction. Of the two genera *Heterangium* appears to be the more ancient, and certainly stands nearer to the Filicinean ancestry. *Lyginodendron*, while still retaining conspicuous Fern-like characters, has advanced much further on Cycadean lines."[1]

The generic name *Lyginodendron* was proposed in 1843 by Mr. Gourlie for a piece of fossil plant which he regarded as a new form, but did not attempt to describe scientifically. Williamson in 1873 applied Gourlie's term to certain plant fragments which he investigated from the calcareous nodules ("coal balls") of Lancashire. The plant so named by Williamson had been previously described by Binney in 1866 as *Dadoxylon Oldhamium*. Three years later Williamson proposed a new name, *Dictyoxylon*, for Binney's plant in place of *Dadoxylon*, a genus in which the Oldham specimen could not be included. Finally Gourlie's name was adopted, in the belief that this older generic designation had been assigned to a plant identical with the much more perfectly preserved Lancashire examples.

So far all specimens of *Lyginodendron* have been included under one specific name, *L. Oldhamium* Will. The stems of this plant may be readily recognised in transverse section by the characteristic structure of the outer cortex, and by the histological features of the central cylinder and leaf-trace bundles. The plant is monostelic, and in a young stem the stele consists of an axial parenchymatous pith with nests or groups of dark and thick walled cells. At the periphery of this tissue occur several detached strands of collateral groups of primary xylem and phloem, the former consisting of scalariform, reticulate, and spiral tracheæ, with a very little parenchyma, and the latter of thinner-walled elongated elements and parenchymatous cells, with

[1] Williamson and Scott, p. 769.

scattered secretory sacs. Owing to the presence of a zone of secondary xylem and phloem, the primary phloem is usually crushed and indistinct, having been separated from the primary xylem by the interpolation of the secondary vascular tissue. One of the most important characteristics of the primary group of xylem is the position of the protoxylem; the narrow spiral tracheids occur just internal to the outer edge of each xylem group, and thus occupy an intermediate position, enabling us to distinguish a small group of centrifugally developed scalariform xylem elements and a larger group of centripetally developed pitted tracheæ.

Each of the primary strands of xylem and phloem is a leaf-trace, and in a series of transverse sections it is possible to follow a bundle in its passage from the petiole to the central cylinder of the stem. The course of these foliar bundles is especially interesting; each extends through about ten internodes, five internodes being traversed by the leaf-trace as it moves outwards from the periphery of the pith to the edge of the secondary wood, and five more in its course through the pericycle and cortical tissues. A trace-bundle on its way through the secondary xylem consists of a primary strand and an arc of secondary xylem tracheæ, but as it passes further out through the stem tissues the secondary arc disappears and the trace divides into two distinct bundles. Finally in the petiole the twin bundles are frequently reunited. The collateral structure of the leaf-trace is replaced by a concentric arrangement, of the phloem and xylem as the strand reaches the leaf-stalk base.

The secondary vascular tissues met with in practically all stems of *Lyginodendron* consist of radiating rows of pitted tracheæ, separated by numerous large medullary rays, and of narrow phloem cells associated with sieve-tube like elements. Secretory sacs are fairly common in both xylem and phlœm rays. In several specimens the characteristic tabular cells of the cambium have been preserved, and there can be no doubt as to the perfectly normal manner of development of the secondary wood and bast. External to the phloem, and constituting the limits of the

stele, there is a multilayered pericycle made up of short-celled parenchyma, containing nests of sclerous cells and numerous secretory sacs. In most cases the pericycle tissues are succeeded towards the exterior by a deep-seated periderm, which arose at an early stage of secondary thickening from a phellogen developed in the pericycle. The extra-stelar region of the stem may be conveniently described as being made up of an inner and outer cortex; the former consists of parenchyma with scattered secretory cells and occasional sclerous nests. The outer cortex presents a very characteristic appearance, being made up of alternate radiating bands of dark sclerenchyma, and lighter-coloured, thin-walled, parenchyma containing secretory sacs. From the peripheral cells of the cortex plint emergences are here and there developed.

Mention has been made of petioles attached to the *Lyginodendron* stems. The nature of these appendages is of special interest as regards the affinities of the plant.

In 1872 Williamson suggested a possible connection between certain structures described under the generic name of *Edraxylon* and the stem of *Lyginodendron.* Subsequently the genus *Rachiopteris* was substituted for *Edraxylon,* and thus the *Lyginodendron* leaves were included among true fern fronds. There is now direct proof that *Rachiopteris aspera* Will. is the petiole of *Lyginodendron.* The form of the ultimate segments of the frond is that long known to palæobotanists under the provisional generic name *Sphenopteris.* The petiole is made up of a ground-mass of parenchyma with alternate radiating strands of sclerenchyma and thin walled tissue at the periphery. Long secretory sacs traverse the inner fundamental tissues, and externally the cortex exhibits gland-like out-growths or emergences similar to those in *Lyginodendron* stems. The vascular bundle of the leaf-stalk is of the typical concentric form, and usually consists of a mass of V-shaped xylem containing several protoxylem groups surrounded by a thin-walled and small-celled phloem. External to the phloem a more or less well-marked pericycle has been recognised, but no distinct bundle-sheath. In addition to the structural

features of the main petiole and its branches, the histology of the leaf lamina has been described in some detail. The veins in the lamina seem to be of the collateral type, and the mesophyll is composed towards the upper surface of closely arranged cells elongated at right-angles to the epidermis, and towards the lower of more loosely disposed and less regular cells. Stomata have also been recognised in transverse sections of these sphenopteroid pinnules.

Finally the adventitious roots of this interesting genus have been thoroughly investigated. In certain regions of the stem adventitious roots are given off on all sides, both from nodes and internodes; their origin is clearly endogenous, and their histological features such as characterise true root structures. The roots, like the petioles, were originally described as a distinct genus, and named by Williamson *Kaloxylon Hookeri*. The stele of the root consists of two to eight centripetally developed groups of xylem with conjunctive parenchyma, alternating with groups of smaller cells, consisting partly of short parenchyma and in part of narrow elongated elements. Surrounding the xylem and phloem is a one-layered pericycle and a layer of stouter cells with the characteristic radial markings of endodermal cells occasionally visible. External to the innermost layer of the cortex, we have a broad zone of lax parenchyma with conspicuous and abundant secretory sacs, and externally a peculiar epidermal layer made of two or three rows of thin-walled cells. Many of the roots examined show a zone of secondary xylem and phloem, formed in a manner essentially identical with the method of development of secondary vascular tissues from a typical root cambium.

Having thus briefly referred to some of the more striking anatomical characteristics of *Lyginodendron*, it remains to describe in a few words the habit of the whole plant and to discuss its affinities with recent forms. So far we are without any satisfactory evidence as to the nature of the reproductive organs. To quote Williamson and Scott's words:[1] "We must, therefore, picture *Lyginodendron* to

[1] Williamson and Scott, p. 743.

ourselves as having a tall, upright stem rising to a height of several feet and bearing somewhat remote, spirally arranged, highly compound, fern-like leaves. The base of the stem, where the adventitious roots were given off, must have been buried for some depth in the earth or mud. . . . The stem is mechanically well constructed, and thus fitted to maintain an upright position while bearing abundant foliage. We have no distinct evidence for any rhizome-like organs, but it is possible that some of the small shoots which are rather deficient in sclerenchyma may have been creeping or subterranean." Certain interesting examples of anomalous structures in *Lyginodendron* stems have been figured and described, but it is impossible to deal with these in the present article.

Affinities. The leaf-trace bundle system of the stem agrees in certain respects with that of *Osmunda.* In both genera the stele possesses a ring of collateral primary bundles, and in both there is good evidence for believing that in the lower stem internodes the xylem has the form of a continuous ring enclosing a central pith. Another point of contact between the fossil plant and recent ferns is afforded by the Gleicheniaceous genus *Platyzoma,* in which the monostelic stem possesses a distinct pith. The protoxylem of *Lyginodendron* is of the same type as that of the foliar bundles of recent cycadean petioles, and in some cases also of the stem bundles of Cycads. The term "mesarch," proposed by Solms-Laubach, has been adopted for this particular form of bundle. The characteristic feature of mesarch bundle, is that the protoxylem is not on the inner or outer limit of the primary xylem tracheæ, but occupies an intermediate position between the primary centripetal and primary centifugal xylem elements.

The secondary wood and bast are similar in a striking degree to the corresponding tissues in cycadean stems. As regards the cortex, the emergences of the peripheral tissues suggest those of *Alsophila* and other recent ferns. Passing to the petiole, we lose sight of the more distinctly cycadean affinities, and find an obvious correspondence with the anatomy of recent ferns. The concentric bundle is clearly

fern-like; the absence of a definite endodermis recalls the leaf stalks of *Marattiaceæ*. The foliage is equally suggestive of ferns in form and structure. In the roots, as regards the primary structure, we have a further illustration of a fern alliance, and especially with Marattiaceous genera. The above comparisons are sufficient to conclusively demonstrate the synthetic character of the fossil genus.

The second form described by Williamson and Scott must be dismissed in a few words. In 1871 certain stem fragments were discovered amongst the well-known material from Burntisland, which were subsequently referred to Corda's genus *Heterangium*. Of this genus we now possess a comparatively full knowledge of two specific form, *H. Grievii*, Will. and *H. tiliæoides*, Will. The central cylinder of the stem consists of an axial mass of primary xylem traversed by anastomosing bands of parenchyma. Towards the periphery of the central region distinct groups of tracheæ may be distinguished, containing protoxylem elements in the position characteristic of mesarch bundles. As in *Lyginodendron*, these peripheral vascular strands are true leaf-traces. There is a clearly marked pericycle, and external to this a wide inner cortex of parenchyma, containing characteristic horizontal plates of sclerous tissue, followed by an outer cortex traversed towards the periphery by radially disposed bands of sclerenchymatous fibres. In most cases the primary xylem and phloem tissues are surrounded by a zone of secondary wood and bast with numerous medullary rays. The species *Heterangium tiliæoides* is especially interesting as exhibiting a remarkably perfect state of preservation of the sieve-tubes with their lateral sieve-plates. The cambium is occasionally extremely well preserved. The petioles and pinnules are similar to those of *Lyginodendron*, but it has not been possible to investigate their structure to quite the same extent.

Again, in its adventitious roots, *Heterangium* agrees closely with the preceding genus. With the exception of the secondary xylem and phloem, the stem of *Heterangium* is "essentially that of a monostelic fern of the *Gleichenia*

type". The occurrence of pitted tracheids, the collateral arrangement of the xylem and phloem in the leaf-trace bundles in their course through the stem tissues, and the differentiation of the peripheral stelar tissues into distinct leaf-trace strands, are features peculiar to *Heterangium* as compared with recent ferns. No great stress should be laid on the much more considerable development of secondary tissue in the fossil genus than in living ferns. *Botrychium* and *Helminthostachys* both illustrate to a certain extent the power of recent ferns to increase by secondary thickening, and the comparison of other Palæozoic types with their nearest living allies has taught us not to attach any great importance to secondary thickening as a character of primary taxonomic value.

It is of interest to note, that in *Heterangium* the resemblance of the secondary vascular tissues to those of Cycads extends to details of the sieve-plates.[1]

Williamson and Scott have clearly shown that in different parts of their structure the two genera *Heterangium* and *Lyginodendron* reveal distinct points of agreement with *Gleicheinaceæ*, *Osmundaceæ*, *Marattiaceæ*, *Ophioglosseæ*, and *Cycadaceæ*. Without suggesting that these Palæozoic types are the actual ancestors of existing Cycads, the authors regard them as "derivatives of an ancient and 'generalised' Fern Stock, which already shows a marked divergence in the Cycadean direction". The two plants described above, with other genera previously known, clearly point to the existence of a fossil group of plants "on the borderland of ferns and *Cycadaceæ*".[2]

It would be easy, did space permit, to discuss the structure and affinities of several of the Palæozoic plants belonging to this generalised group. The genera so ably and lucidly dealt with in Williamson and Scott's splendid memoir, afford excellent examples of the data which palæobotany is able to contribute towards the solution of developmental problems. The value of such work as this can hardly be overestimated; the evidence which is in this

[1] Williamson and Scott, p. 766.

[2] *Ibid.*, p. 769.

manner adduced rests on the best foundation, and must indubitably lead to a fuller recognition of the value of palæobotanical research as a factor of primary importance in phylogenetic inquiries.

In addition to the various points suggested in the description of these two extinct plants, and referred to in the foregoing summary, there are at least two reflections worthy of mention. In the first place, the work of many palæobotanists has clearly emphasised the need and importance of a more intimate acquaintance with the morphology of existing Cycads. Secondly, it would appear certain that among the numerous leaves of Palæozoic plants which it has been the general custom to regard as typical fern fronds, there must be some which belong to stems in which Cycadean characters more or less predominated. The probable connection of many "Cycadean" fronds with Bennettitean stems illustrates an analogous case among Mesozoic plants.

A word of the highest praise is due to Mr. Brebner for the admirable illustrations accompanying Williamson and Scott's memoir;[1] it would be difficult indeed to obtain more accurate and artistic reproductions of the almost incredible perfection of detail exhibited by sections of Carboniferous plants.

A. C. SEWARD.

[1] Williamson, W. C., and Scott, D. H. "Further observations on the Organisation of the Fossil Plants of the Coal-Measures." Part iii. *Lyginodendron* and *Heterangium*. *Phil. Trans. Royal Society*, vol. clxxxvi., B., pp. 703-729, pls. 18-29, 1896.